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Seattle, Washington

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HEAT EXCHANGE IN THE YELLOWFIN TUNA, *THUNNUS ALBACARES*, AND SKIPJACK TUNA, *KATSUWONUS PELAMIS*, AND THE ADAPTIVE SIGNIFICANCE OF ELEVATED BODY TEMPERATURES IN SCOMBRID FISHES

JEFFREY B. GRAHAM[1]

ABSTRACT

Thunnus albacares and *Katsuwonus pelamis* are warm-bodied fish and use retia mirabilia as countercurrent heat exchangers. Both species have four sets of lateral exchangers, two epaxial and two hypaxial, each consisting of a large cutaneous artery and vein and rete. *Katsuwonus pelamis* has a central exchanger, located within the haemal arch, which consists of the dorsal aorta, the posterior cardinal vein, and a large vertical rete. The central heat exchanger in *T. albacares*, while also in the haemal arch, is simpler, consisting of two small "wing-shaped" retia on either side of the dorsal aorta and cardinal vein.

The adaptive significance of the specialization for heat conservation is discussed. Body temperatures, thermal profiles, and the natural histories of different warm-bodied species are compared, and warm fishes are contrasted with scombrids that do not conserve heat. The skipjack tunas, *Euthynnus* and *Katsuwonus*, have well-developed central heat exchangers and are much warmer than *T. albacares*. Higher body temperatures in skipjacks seems related to their requirement for a higher basal swimming speed and their faster burst speed.

Comparisons on the basis of existing knowledge about the two phyletic groups of *Thunnus* reveal few differences in swimming ability or factors related to locomotion. The bluefin group, consisting of *T. thynnus*, *T. maccoyii*, and *T. alalunga*, however does contrast with the yellowfin group (*T. albacares*, *T. atlanticus*, and *T. tonggol*) by maintaining generally higher body temperature differentials, having incomplete vertebral circulation through the absence of a posterior cardinal vein, and occurring at higher latitudes.

Scombrids (mackerels, bonitos, and tunas) are pelagic, oceanic fishes that are highly adapted for continuous swimming. Some of the more advanced scombrids (principally frigate mackerels, *Auxis;* skipjack tunas, *Euthynnus* and *Katsuwonus;* and tunas, *Thunnus*) have evolved the capacity to conserve heat generated by the continuous metabolic activity of their swimming muscle and thus maintain body temperatures that are warmer than ambient seawater (Carey et al. 1971; Carey 1973). There has been convergent evolution for this specialization in mackerel sharks (Isuridae) a highly active, continually swimming group (Carey and Teal 1969a).

Warm-bodied fish retain heat by using retia mirabilia (= wonderful network) as countercurrent vascular heat exchangers. The principal advantage of a high and fairly constant body temperature is facilitation of continuous swimming by increasing the frequency of muscular contractions, thus increasing available swimming power (Carey et al. 1971). Also, warm-bodied fish probably achieve a marked independence from environmental temperature permitting them to make rapid vertical and latitudinal migrations without the necessity of thermal acclimation.

In their extensive review of warm-bodied fish, Carey et al. (1971) described two types of heat exchanger, lateral and central. Lateral heat exchangers (Figure 1) are present in many warm-bodied species but are best developed in the genus *Thunnus* where they consist of four sets of longitudinal subcutaneous arteries and veins (two epaxial and two hypaxial), each with adjoining layers of retial vessels that penetrate the red muscle near the midplane (Gibbs and Collette 1967; Carey et al. 1971). Large, highly developed central heat exchangers (Figure 1) are found in *Euthynnus*, *Katsuwonus*, and *Auxis*. These are located below the vertebral column, in the haemal arch, and consist of a large vertical rete formed from branches of the dorsal aorta and the posterior

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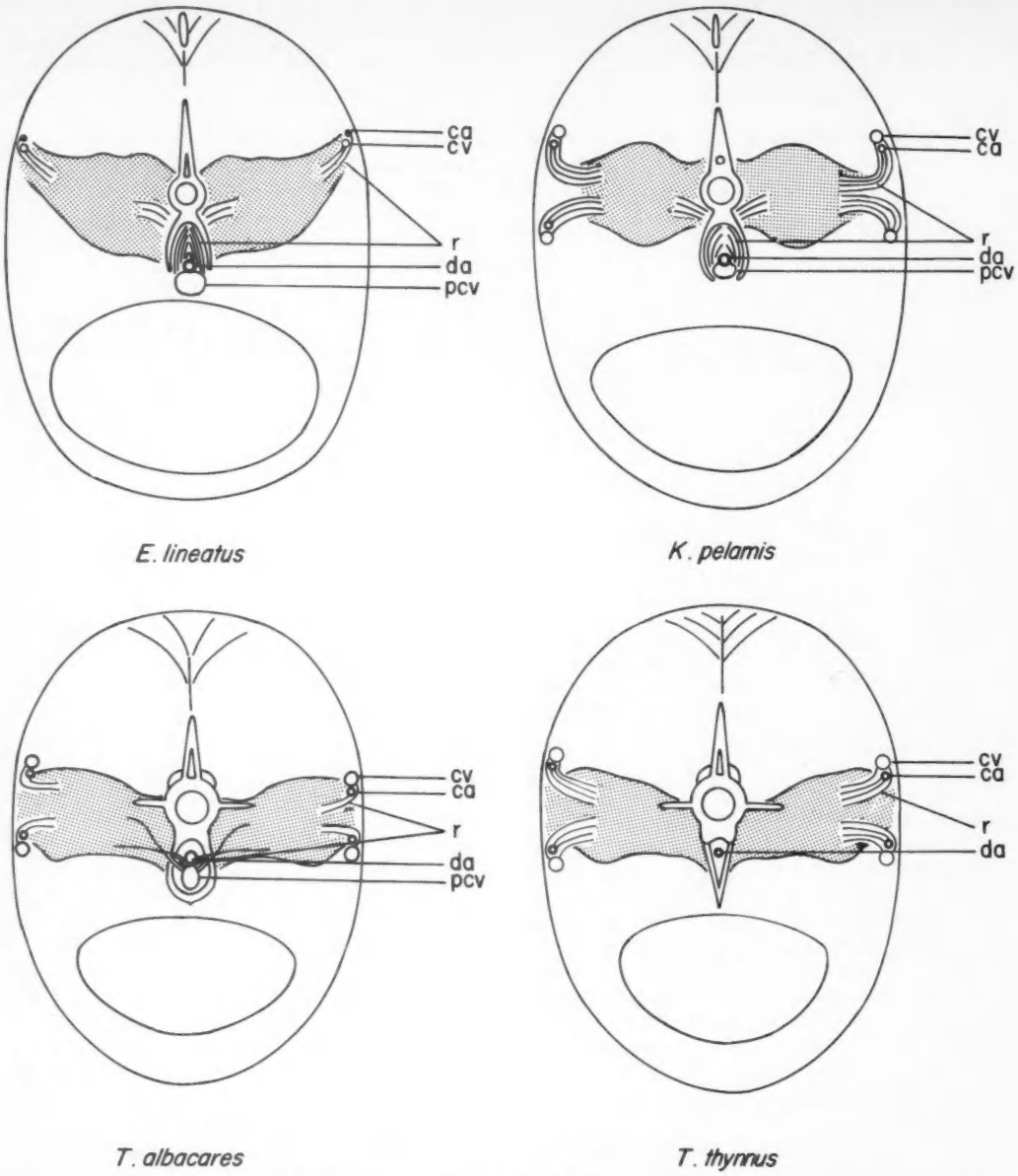

FIGURE 1.—Transverse sections of four warm-bodied species showing the position of central and lateral retia mirabilia (r) that function as vascular heat exchangers. The major blood vessels supplying retia are: dorsal aorta (da), posterior cardinal vein (pcv), cutaneous arteries (ca), and veins (cv). Veins are shown with larger diameters and thinner walls. Red muscle distribution (shaded areas) is also depicted. Noted that the position of cutaneous arteries and veins in *Euthynnus lineatus* is reversed compared to that in other species and that only an epaxial pair is present. Also, *Thunnus thynnus* does not have a posterior cardinal vein. Frigate mackerels (*Auxis*) are not shown but are very similar to *Euthynnus*. Data contained in this figure are from various sources cited in the text.

cardinal vein (Kishinouye 1923; Godsil 1954; Carey et al. 1971; Carey 1973; Graham 1973).

Kishinouye (1923: 377; see discussion of *Neothunnus*, a synonym of *T. albacares*) described a special subspinal vascular plexus or "kurochiai" in the yellowfin tuna, *T. albacares* (Bonnaterre), and recent studies have indicated that this structure is a central heat exchanger (Carey et al. 1971; Carey 1973). The kurochiai has not been fully described, nor has the relationship between it and *T. albacares'* well-developed lateral heat exchangers been considered. Body temperatures of fresh-caught and swimming yellowfin tuna are known to be less than those of skipjack tunas and some other tuna when measured under similar conditions (Barrett and Hester 1964; Carey and Teal 1969b; Stevens and Fry 1971; Carey 1973), but where heat is distributed in the body (thermal profiles) has not been determined for either *T. albacares* or the skipjack tuna *K. pelamis* (Linnaeus).

The purpose of this study is to investigate the relationship between body temperature and the types of heat exchanger in *T. albacares*. The patterns observed for this species and *K. pelamis* are compared with those of other warm-bodied fish. Body temperatures and thermal profiles of fresh-caught *T. albacares* and *K. pelamis* are reported, and their central heat exchangers are described. The general structure and circulation pattern of these species' heat exchangers are compared with those of the bluefin tuna *T. thynnus*, and other skipjack tunas, *Euthynnus*, and are discussed in terms of their relation to differences in body temperature, morphology, swimming capability, and the natural history of these species. Studies of this type may enable us to understand why there are different kinds of heat exchangers and how these evolved.

MATERIALS AND METHODS

Eleven *T. albacares* (360 to 700 mm fork length; weight, 1 to 5 kg) and four *K. pelamis* (500 to 600 mm, 3 to 4 kg) were caught by surface trolling in the Gulf of Panama and brought on board within 30 to 90 s of being hooked. Red and white muscle temperatures of these specimens were immediately taken with a fast-reading hypodermic thermistor probe (Yellow Springs Instrument No. 513)[2] that had been calibrated against a mercury thermometer. Measurements were made deep (near the vertebrae), midway from the vertebrae to the skin, and subcutaneously at several positions along the fishes' lateral midplane, from the operculum to the tail, in order to determine the relative contribution of the lateral and central heat exchangers to heat distribution. All temperatures were rounded to the nearest 0.5°C. Body temperatures of shaded fish remained fairly constant during the first 10 min after capture, and all measurements were made within this time.

A criticism that has been directed against the measurement and interpretation of temperature data from fresh-caught fish is that burst swimming to catch a troll lure, or frenzied swimming, together with struggling once hooked may increase body temperatures above typical values. This probably has some validity, but the effects of struggling and handling seem generally overrated. With telemetry, Carey (1973) has shown that free-swimming *T. thynnus* have body temperatures very similar to captured fish. Also, Barrett and Hester (1964) found that immediately captured yellowfin tuna and those that had been tethered for a few minutes had similar temperatures.

Large frozen *T. albacares* (800 to 1,400 mm, 8 to 42 kg) were obtained from a commercial fishing vessel, and a range of sizes was dissected to determine red muscle distribution, the position, size, and structure of the heat exchangers, and the dimensions of retial vessels. Specimens of *K. pelamis* were also dissected, and measurements were made.

RESULTS

Body Temperatures

Average deep, intermediate, and subcutaneous red muscle temperatures of eight *T. albacares* (caught in surface water of 28.5°C) were 30.5°, 30.5°, and 29.5°C. Three specimens caught in 30°C water had average deep body temperatures of 32.5°C. Elevated temperatures in *T. albacares* occur along the body from the pectoral fins to as far as the third or fourth finlet. The warm region also extends laterally through a large portion of the red muscle. Highest body temperatures were always found in the red and white muscle along and near the lateral midplane of the body. *Katsuwonus pelamis* is warmer than *T. albacares*, and its warm

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

region extends laterally to just below the skin. The average deep, intermediate, and subcutaneous red muscle temperatures of four *K. pelamis* (caught in 28.5°C surface water) were 35°, 35°, and 33°C. Deep white muscle temperatures in these fish averaged 34°C; brain temperatures were 33°C. The temperatures reported here for *T. albacares* and *K. pelamis* are in good agreement with those found for these species by other investigators (Barrett and Hester 1964; Stevens and Fry 1971).

Heat-Exchanger Structure and Red-Muscle Distribution

Thunnus albacares

The distribution and structure of the lateral heat exchangers found for *T. albacares* in this study agree fully with those described by Gibbs and Collette (1967) and are summarized here with new notes on variations related to size. Epaxial and hypaxial arteries and veins subdivide from their respective trunks at about vertebrae no. 10 and extend along the body to about two-thirds of the way from the second dorsal fin to the tail (vertebrae no. 29 or 30) where they are rejoined by a commissure. One row of retial vessels originates from the lateral edge of each artery and vein, and this is consistent with the observations of Kishinouye (1923, as *Neothunnus*). *Thunnus albacares*' lateral retia are long and strongly curved towards the center of the body. Retial curvature was not observed in specimens smaller than 3 kg. Cutaneous vessel diameters increase dramatically with increased size, ranging from 0.5 to 1.0 mm (artery and vein) in a 1.1-kg specimen to 6.0 to 8.0 mm in a 42-kg fish. Retial vessels ranged from 0.05 to 0.1 mm in diameter.

The central heat exchanger in *T. albacares* extends from the first to the second dorsal fins (vertebrae no. 8 or 9 to 20) and is situated immediately below the vertebrae in the haemal arch. This structure is composed of the dorsal aorta, the posterior cardinal vein, and their small vessels that form two "wing-shaped" retia (Figure 2). Diameters of the dorsal aorta and posterior cardinal vein only increase slightly with increasing size, ranging from 1.5 to 3.0 mm in a 2.7-kg fish to 3.5 to 4.0 mm in a 42-kg specimen. This contrasts markedly with the large weight-related change in the diameters of the lateral blood vessels. The central retia originate as thick bundles in the haemal arch, then extend supralaterally and pass through vertebral foramina into the red muscle. In the muscle these vessels flatten into broad continuous sheets of alternating veins and arteries (0.1 to 0.2 mm in diameter) that are only one layer thick (Figure 2). This layer penetrates far into the muscle, from 18 mm in a 2.7-kg fish to 40 mm in a 42-kg fish.

Red muscle in *T. albacares* appears in thin bands along each side of the fish at the level of the vertebrae (Figure 2). Only red fibers from the hypaxial muscles actually reach the vertebrae, but epaxial and hypaxial muscle both extend well toward the fishes' side. Longitudinally, red muscle extends from behind the transverse septum (vertebrae no. 6 or 7) to as far as the fifth finlet (vertebrae no. 28 or 29) and is fairly uniform in thickness and shape (cf. Kishinouye 1923, Plate XVII, as *Neothunnus*). As was found for *E. lineatus* (Graham 1973) and, as would be expected, there is good agreement in the lineal distribution of red muscle and the lateral and central heat exchangers of *T. albacares*.

Katsuwonus pelamis

Except for its higher position in the body, the central exchanger of *K. pelamis* (Figure 3) is very similar to that of *Euthynnus* and *Auxis*, consisting of the closely associated dorsal aorta and posterior cardinal vein and a thick vertical rete, all in the haemal arch (Kishinouye 1923; Godsil 1954; Graham 1973). Just posterior to the pectoral fins in a 580-mm (about 4 kg) specimen, the following vessel diameters were measured: dorsal aorta, 2.0 mm; posterior cardinal vein, 4.0 mm; retial vessels, 0.05 to 0.1 mm. At its center (Figure 3), vessels in the central rete of this fish were 8.0 mm long.

Lateral heat exchangers are better developed in *K. pelamis* than in either *Euthynnus* or *Auxis* (Figure 1). Both epaxial and hypaxial sets of cutaneous vessels, with retia, are present, but they are further apart than in *T. albacares* (Figure 1), reflecting the laterally thicker wedge of red muscle in *K. pelamis* (see below). The cutaneous vessels are smaller than in *Thunnus*. The most developed retial vessels occur anteriorally but are variable in their position, length, and the direction they penetrate red muscle (cf. Godsil and Byers 1944, Figure 15).

Red muscle in *K. pelamis* is thicker than in *T. albacares* but does not appear to extend as far into the tail. In a transverse section (Figure 3), both

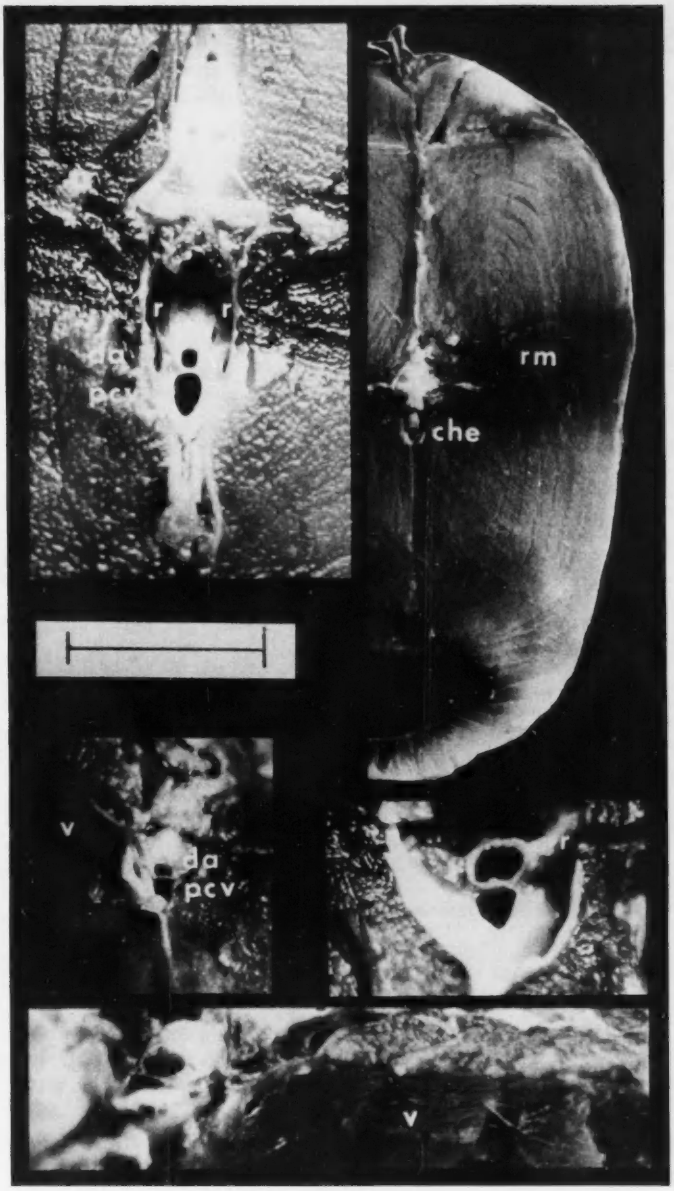

FIGURE 2.–Central heat exchanger of *Thunnus albacares*. (Top right, scale = 6.5 cm): Transverse sections showing the position of red muscle (rm) and the central heat exchanger (che). (Top left, scale = 1.5 cm): Transverse section of the che showing the dorsal aorta (da), posterior cardinal vein (pcv), and retia (r). (Middle right, scale = 2 cm): A close view of the che showing the da, pcv, and two wing-shaped retia that proceed supralaterally from the vessels. (Middle left, scale = 1.2 cm): A ventrolateral view of the da, pcv, and the sheet of vessels (v) outside the haemal arch that penetrate red muscle. (Bottom, scale = 2.0 cm): Ventrolateral view showing the che on the left and the thin sheet of vessels in red muscle.

hypaxial and epaxial red muscle reach the vertebrae. Longitudinally, shape as well as thickness of red muscle varies at different points (cf. Kishinouye 1923, Plate XVII). Generally, red muscle in *K. pelamis* appears to have more ligaments than *T. albacares*. In both species the myomeres are continuous through red and white muscle (Figures 2, 3), but red and white muscle are easily distinguished and separate with slight teasing.

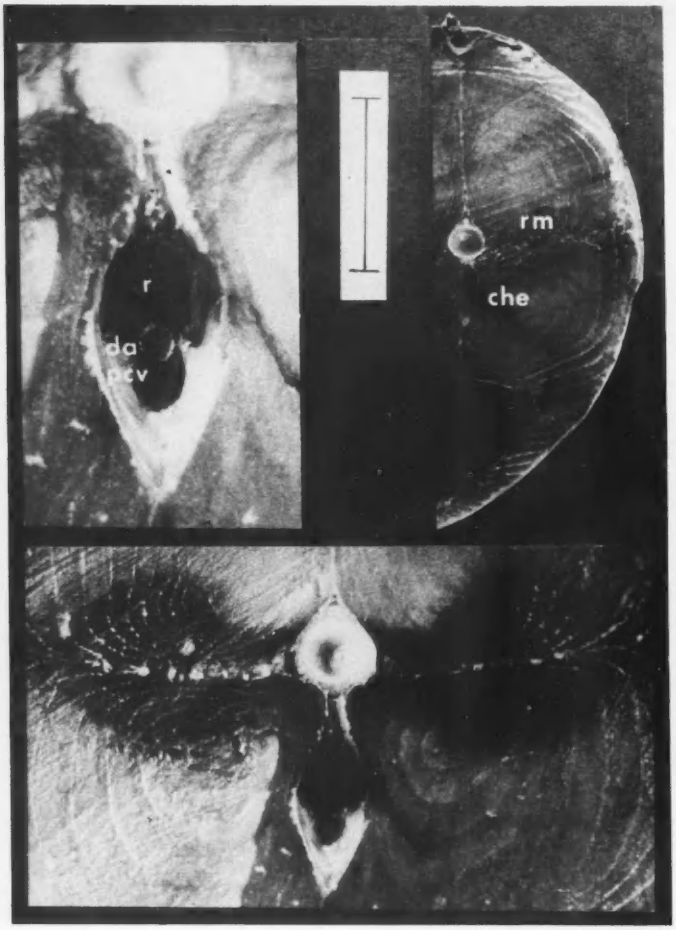

FIGURE 3.–Central heat exchanger of *Katsuwonus pelamis*. (Top right, scale = 5.6 cm): Transverse section showing the position of the central heat exchanger (che) and red muscle (rm). (Top left, scale = 1.1 cm): Close view of the rete (r), the dorsal aorta (da), and the posterior cardinal vein (pcv) in the haemal arch. (Bottom, scale = 1.9 cm): Red muscle and the central heat exchanger.

COMPARISON OF *KATSUWONUS, EUTHYNNUS, AUXIS,* AND *T. ALBACARES*

Differences in Heat Exchangers

Central heat-exchanger differences can be summarized as follows: *Katsuwonus, Euthynnus,* and *Auxis* have only a single vertical rete whereas *T. albacares* has two much smaller retia. *Thunnus albacares'* central exchanger is immediately below the vertebral centrum (Figures 1 and 2) while in *K. pelamis* it is lower, about midway between the vertebrae and the coelomic cavity, and in *Euthynnus* and *Auxis* it is quite low, occurring just above the coelom (Kishinouye 1923; Godsil 1954; Graham 1973). In *E. lineatus* and *E. alletteratus,* and *K. pelamis* that I have examined, and in *Auxis* (Godsil 1954), the dorsal aorta is actually embedded in the dorsal side of the posterior cardinal vein and is surrounded by a vast network of retial vessels which in effect bathes the aorta in venous blood. This structure has been interpreted as allowing the rete to occupy a full arc over the vessels, thus maximizing its heat-exchanging area (Graham 1973).

Both *K. pelamis* and *T. albacares* have two pairs of lateral exchangers. *Katsuwonus* has two

somewhat variable rows of retial vessels in each lateral exchanger while *T. albacares* only has one. *Euthynnus* and *Auxis* (Figure 1) have only a small pair of epaxial heat exchangers.

Thermal Profiles of Fish with Central Exchangers

Lateral midplane thermal profiles of *T. albacares* and *K. pelamis*, taken in the red muscle just posterior to the pectoral fins, illustrate general differences in thermal profiles and body temperatures between these species, *E. lineatus*, and *T. thynnus* (Figure 4). *Katsuwonus* and *Euthynnus* have much warmer core temperatures than *T. albacares*, but warmest temperatures in *Euthynnus* are restricted to a fairly narrow zone around the vertebral column. *Euthynnus'* profile therefore seems related to its poorly developed lateral exchangers (also red muscle is very thick in the center and thinner laterally, Figure 1) and, based on structural similarities, this type of thermal profile would be predicted for *Auxis*. *Katsuwonus* on the other hand, with its lateral exchangers has heat widely distributed across its body.

Thunnus albacares, with a small central exchanger and well-developed lateral exchangers has a widely distributed warm region although it is much cooler than *K. pelamis* and *E. lineatus* (Figure 4). The dimensions of *T. albacares'* cutaneous vessels increase at a much faster rate with increased body weight than do the dorsal aorta and posterior cardinal vein, and in larger fish a greater proportion of blood flow would occur through lateral vessels which might change the thermal profile.

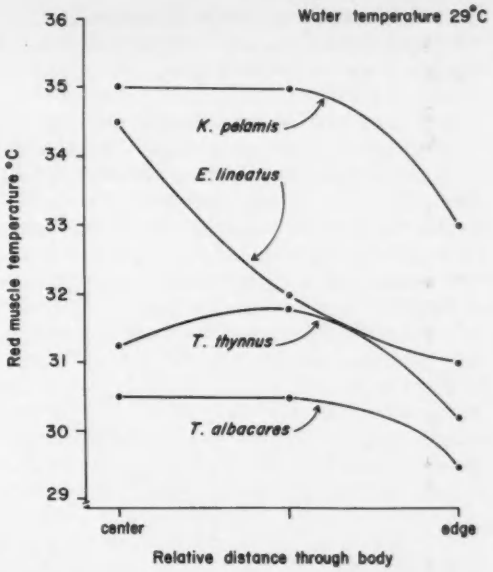

FIGURE 4.—Lateral midplane thermal profiles from the center (near the vertebrae) to the edge (subcutaneous) of red muscle in four species of warm-bodied fish. (Data for *Thunnus thynnus* were provided by F. G. Carey, that for *Euthynnus lineatus* are from Graham 1973).

COMPARISONS WITHIN THE GENUS *THUNNUS*

Heat Exchangers and Thermal Profiles in *T. albacares* and *T. thynnus*

Comparative studies of the vascular anatomy of *Thunnus* show different levels of structural complexity in the heat-exchanging systems (Kishinouye 1923; Godsil and Byers 1944; Gibbs and Collette 1967) which relate to thermal profiles and body temperatures. In *T. thynnus*, lateral heat exchangers are used solely (Carey and Teal 1966). Two rows of retial vessels emanate from each cutaneous artery and vein (only one row occurs in *T. albacares*), and these extend axially for a long distance (Carey et al. 1971). Reliance upon cutaneous circulation is so extensive in *T. thynnus* that the dorsal aorta is reduced in diameter and the posterior cardinal vein is absent. In warm water *T. thynnus* is about the same temperature as *T. albacares*, but its thermal profile (Figure 4) reflects the exclusive presence of lateral heat exchangers in that warmest temperatures are found in the middle of the muscle, while the center of the fish is cooler (Carey et al. 1971). (Again, thermal profiles probably change with body size.)

Anatomical Features and Phyletic Groupings Related to the Presence or Absence of Complete Vertebral Circulation

In their comprehensive study of the genus *Thunnus*, Gibbs and Collette (1967) recognized seven species which, on the basis of 18 characters, were separated into two phyletic groups: the bluefin tuna group, *T. thynnus*, *T. alalunga*, and *T.*

maccoyii; and the yellowfin tuna group, *T. albacares, T. atlanticus,* and *T. tonggol.* (The seventh species, *T. obesus,* has traits in common with both groups and will be discussed later.) Several of the characters used (Gibbs and Collette 1967, Table 4) to distinguish these groups are related to the presence or absence of complete vertebral circulation (both a dorsal aorta and posterior cardinal vein present). The yellowfin tuna group has a posterior cardinal vein, the bluefin tuna group does not. Another striking difference is the presence of large striations and vascular cones on the livers of fish in the bluefin tuna group. The importance of this is discussed below.

There are several structural modifications in the vertebrae of the yellowfin tuna group which permit the passage of more or larger blood vessels through the haemal arch. Prezygapophyses arise far more ventrad on the haemal arch, postzygapophyses are longer, and the inferior foramina are larger (Gibbs and Collette 1967, Figures 10-13). In describing these vertebrae, Gibbs and Collette (1967:80) remarked that the development of the vertebral openings and processes in the yellowfin tuna group is almost as complex as that in *Auxis, Euthynnus,* and *Katsuwonus.* The presence of complete vertebral circulation and appropriate modifications in the vertebral column suggested to me that other species in the yellowfin tuna group, in addition to *T. albacares,* may have central heat exchangers. I have examined a preserved section of vertebral column from *T. atlanticus* (collected in the Gulf of Mexico and sent to me by F. G. Carey) and *T. tonggol* (obtained by G. Sharp) both of which have a central exchanger like that of *T. albacares.*

ADAPTIVE SIGNIFICANCE OF DIFFERENT HEAT EXCHANGERS, BODY TEMPERATURES, AND THERMAL PROFILES

Heat exchangers in *T. albacares* differ from those of *K. pelamis* and *E. lineatus,* and among these three species, there are marked differences in body temperatures and thermal profiles (Figure 4). *Thunnus albacares* and *T. thynnus* also have different heat exchangers, different body temperatures, as well as different thermal profiles depending on body size. Are there morphological features related to locomotion, or ecological factors, such as geographical distribution patterns or feeding behavior, that would explain thermal and anatomical differences between *K. pelamis* or *E. lineatus* and *T. albacares* or between species of *Thunnus*?

Comparisons Within the Genus *Thunnus*

The morphologies and locomotion of *T. thynnus* and *T. albacares* have not been compared. There are some data; however it is diffuse and mostly anecdotal, and it does not suggest functional differences in these two species or in the bluefin and yellowfin tuna groups of *Thunnus.*

If species in the yellowfin and bluefin tuna groups are compared on the basis of existing body-temperature data (cf. Carey et al. 1971, Table 1), it is apparent that species in the yellowfin tuna group have lower relative temperatures than those in the bluefin tuna group. Ambient water temperatures are not the same for these different species, and only a general comparison is possible. Still, these differences agree with the known differences in *T. albacares* and *T. thynnus* (Carey and Teal 1969b; Carey 1973) and are suggestive of a general trend of body-temperature differences that might in turn reflect a significant functional difference between the two taxonomic groups.

A feature in the natural history of species in the yellowfin and bluefin tuna groups that clearly separates them, and relates to their anatomical and temperature differences as well, is the water temperature that they normally inhabit. *Thunnus maccoyii* and *T. alalunga* of the bluefin tuna group occur only in cool water while *T. thynnus,* because of its thermoregulatory ability, is wide ranging and may occur in waters from 6° to 30°C but seems most common in the range 16° to 22°C (Gibbs and Collette 1967; Carey and Teal 1969b). Of the yellowfin tuna group, *T. albacares* usually occurs from 20° to 28°C (Schaeffer et al. 1963), and both *T. tonggol* and *T. atlanticus* are strictly tropical species (Gibbs and Collette 1967).

Several facts suggest that incomplete vertebral circulation in the bluefin group is a specialization for living in cooler water and that central heat exchangers are a primitive character related to the occurrence of the yellowfin tuna group in tropical waters. First, central heat exchangers, being restricted to within the haemal arch, are, of necessity small and therefore have limited heat-exchanging capacity. Thus, in cool water, and, given that red muscle is large and located at varying distances away from the vertebrae, a small central heat

exchanger may prove insufficient to maintain a warm temperature. Carey and Teal (1966, 1969b) pointed out the obvious insulative value of having a large lateral heat exchanger between the warm muscle and cool water. Also, in cool water it may not be efficient for heat conservation to pump a large volume of cool blood (from the gills) into the center of the body via the dorsal aorta, and this might explain why the dorsal aorta in *T. thynnus* is small. Indeed, the lower core temperature found in *T. thynnus* may result from the small volume of unheated blood that does flow through the dorsal aorta. Another vascular specialization that appears directly related to the cool-water distribution of the bluefin tuna group is the presence of vascular bundles on their livers which enables these fish to warm their viscera, thus facilitating digestion in cooler water.

A consideration of the bigeye tuna, *T. obesus*, substantiates the idea that central heat exchangers and ultimately complete vertebral circulation are lost as tuna species evolve into cooler habitats. Although *T. obesus* and *T. albacares* have practically the same latitudinal distributions (Gibbs and Collette 1967), the former occurs in deeper and therefore cooler water (Kishinouye 1923:390 as *Parathunnus mebachi*, a synonym for *T. obesus*). This aspect of the distribution of *T. obesus* thus makes it intermediate, in terms of its thermal habitat, to that of the bluefin and yellowfin tuna groups. *Thunnus obesus* is also morphologically intermediate to the bluefin and yellowfin tuna groups of *Thunnus*. It has complete vertebral circulation and vascular bundles on its liver (Gibbs and Collette 1967) yet, F. G. Carey (pers. commun.) who has extensively studied this species reports that it does not have a central heat exchanger. With respect to body temperatures, thermal profiles, and the structure of its lateral heat exchangers, *T. obesus* closely resembles *T. thynnus* (Carey and Teal 1966). Thus for the bigeye tuna, which in terms of adapting to cool water appears to be at an intermediate position between the yellowfin and bluefin tuna groups, a central heat exchanger is not present although complete vertebral circulation persists. With respect to the latter, however, and perhaps underscoring the de-emphasis of vertebral circulation, it is relevant to point out that although *T. obesus* does have a posterior cardinal vein, Godsil and Byers (1944:114) describe it as "relatively small" and note that it fuses anteriorly with the right cutaneous vein.

Elevated Body Temperatures and Locomotion in Skipjack Tunas and *T. albacares*

Studies of scombrid locomotion (Fierstine and Walters 1968; Magnuson 1970, 1973) suggest that elevated body temperature in skipjacks, while related to their requirement for a faster typical (basal) speed, primarily contributes to their higher burst swimming speed.

Magnuson (1970, 1973) pointed out that scombrids are negatively buoyant and that the skipjack tunas, which lack a gas bladder, are even more negatively buoyant than is *T. albacares*. To compensate for this, and to maintain hydrostatic equilibrium, skipjack tunas must swim more rapidly. Magnuson has argued that the need for a faster basal speed correlates well with a significantly higher amount of red muscle found in skipjack tunas (about 8% of body weight in *Katsuwonus* and *Euthynnus*, compared with 7.4% in *T. albacares* of the same size) and with their slightly greater amounts of blood hemoglobin (Magnuson 1973, Table 7).

The amount of red muscle of course bears an important relationship to body temperature. In warm-bodied fish, retia supply blood to red muscle which is highly aerobic. Red muscle is the principal organ used for basal swimming (Rayner and Keenan 1967), and therefore it is the principal site of thermogenesis. (White muscle mainly functions in burst swimming.) Thus skipjack tunas, to maintain a high basal speed, have a large mass of red muscle, and it could be logically concluded that to augment power output, the capacity to conserve heat and keep swimming muscles warm has evolved in skipjack tunas. The difficulty with this idea however is that other scombrids such as the Pacific bonito, *Sarda chiliensis*, have minimum speed requirements as high as those of the skipjack tunas (Magnuson 1973), but are not warm-bodied, nor do they have high hemoglobin levels or large amounts of red muscle. This obviously indicates that elevated body temperatures and high amounts of hemoglobin and red muscle in the skipjack tunas, while contributing to the sustenance of a high basal speed, must have other functions as well.

Further comparison of *Sarda* with *Euthynnus* provides valuable insight to the significance of elevated body temperature to burst swimming. *Sarda velox* and *E. lineatus* (Figure 5) attain about the same size and are morphologically

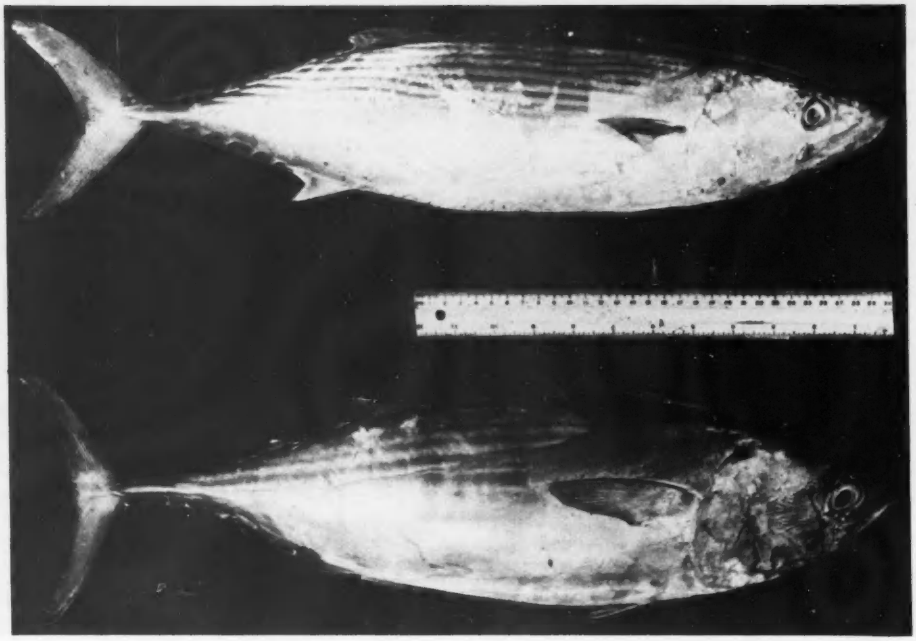

FIGURE 5.–The bonita, *Sarda velox*, (top) and the skipjack tuna, *Euthynnus lineatus* (bottom). Note differences in body shape and pectoral and caudal fin size and shape.

similar. These species also have similar distributions and, in the Gulf of Panama, they occur in the same areas and eat similar prey (crustaceans, squid, and small fishes; pers. obs.) although *Sarda* has a bigger mouth and large teeth. The different mouths and other differences suggest that the swimming capability of these species are also different. *Sarda* has a smaller pectoral fin (Magnuson 1973; Figure 5, this paper) and a lower caudal fin aspect ratio (Fierstine and Walters 1968, Table 7). Its red muscle is not as well developed as that in *Euthynnus* (Fierstine and Walters 1968:17), and *Sarda* has much less blood hemoglobin (Klawe et al. 1963). Finally, a very striking difference exists in the maximum burst speeds of *E. affinis* and *S. chiliensis* (Magnuson 1973, Table 6). In fact, the three warm-bodied species listed by Magnuson (Table 6), all have burst speeds nearly double those of *S. chiliensis*, suggesting that elevated body temperatures, coupled with morphological adaptations, greatly increase the maximum swimming speed. The principal contribution of high body temperature to burst swimming is probably the maintenance of a thermal profile that warms large portions of white muscle.

For *Katsuwonus*, *Euthynnus*, and *T. albacares*, which are all tropical species, there are differences in several structures related to locomotion such as caudal fin aspect ratio and the amount, distribution, and shape of red muscle (Fierstine and Walters 1968). It is reasonable to assume that these differences, combined with elevated body temperature, must confer different capabilities for acceleration, maneuverability, and sustained swimming on different species. One difficulty with the data presently available however is that *T. albacares* grows to be much larger than skipjack tunas, and allometric growth is known or thought to occur in several locomotion-related structures (see discussions by Gibbs and Collette 1967; Magnuson 1973). Without quantitative data on growth patterns of these features, their contribution to locomotion cannot be fully evaluated.

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EXPERIMENTAL STUDIES OF ALGAL CANOPY INTERACTIONS IN A SEA OTTER-DOMINATED KELP COMMUNITY AT AMCHITKA ISLAND, ALASKA

PAUL K. DAYTON[1]

ABSTRACT

Studies on the results of competitive interactions between three kelp canopy guilds were conducted in a community in which herbivorous invertebrates have been largely removed from shallow water (approximately 20 m) by sea otters. Small sea urchins observed in the haptera of kelps all disappeared following the canopy removal, suggesting that the canopy itself offers a modest refuge from their predators. Experiments prove that the largest alga, *Alaria fistulosa*, behaves as a fugitive species with respect to *Laminaria* and *Agarum* species in spite of the structural dominance of a floating canopy. Vegetative regeneration may give *Laminaria longipes* an advantage over other *Laminaria* species, *Alaria*, and presumably *Agarum cribrosum* following disturbances in very shallow water (<5 m). *Laminaria* species suppress *Agarum* growth (and recruitment) in moderate depths (5-20 m) where either *Laminaria* or *Agarum* suppresses growth of red algal turf beneath them, and where both *Laminaria* and *Agarum* must be removed to allow recruitment and growth of *Alaria fistulosa*. Although kelps were observed to depths of 30 m, their lower distribution appears primarily limited by sea urchin grazing.

Few natural communities are so influenced by one population as is the nearshore marine community dominated by the sea otter, *Enhydra lutris* Linn. The nearshore community at Amchitka Island, Alaska, is especially interesting in this regard because for almost 40 yr it has had a sizable sea otter population. This population has been at or near its carrying capacity for at least 20 yr (Kenyon 1969; Estes and Smith 1973), and is thus one of the few localities where the sea otter can be found in a natural balance with the rest of its community. The sea otter exerts its powerful influence in shallow water, where its predation on diverse kinds of invertebrates is remarkably efficient. In addition to drastically reducing populations of motile herbivores (McLean 1962; Ebert 1968; Lowry and Pearse 1973; Estes and Palmisano 1974), the sea otters eat many sessile animals and may release the algae from potential space competition with many potentially competitively important species such as the bivalves *Mytilus edulis*, *Modiolus modiolus*, and *Pododesmus macroschisma*, and the barnacles *Balanus* spp. The algal community at Amchitka Island, then, offers unusual opportunities to evaluate algal-algal interactions in the natural absence of herbivores and animal space competitors. Such interactions might suggest important competitive components of the algal "niches."

The sublittoral association of perennial algae at Amchitka has four separate canopies (Figure 1). *Alaria fistulosa* P. et R. is a conspicuous kelp with long floating fronds that form a canopy on the surface (Kibbe 1915). The thickest *Alaria* canopy is usually found in relatively shallow (< 5 m) water. The second canopy level is composed of the following stipitate *Laminaria* species: *L. groenlandica* Rosenvinge, *L. dentigera* Kjellman, *L. yezoensis* Miyabe, and *L. longipes* Bory. This canopy can be found from the intertidal to depths of approximately 20 m. The third canopy is usually composed of *Agarum cribrosum* Bory with short stripes and large broad fronds lying prostrate on the substratum. This canopy of prostrate kelp occurs between 10 and 20 m. Finally there is a turf composed of numerous species of red algae and occasional clumps of green algae, especially *Codium ritteri* Setch. et Gardn. and *Cladophora* spp. The fact that the canopies tend to occupy nonoverlapping patches in shallow (< 10 m) water suggests that there are competitive interactions between the species comprising the canopies. This paper discusses tests of a series of hypotheses

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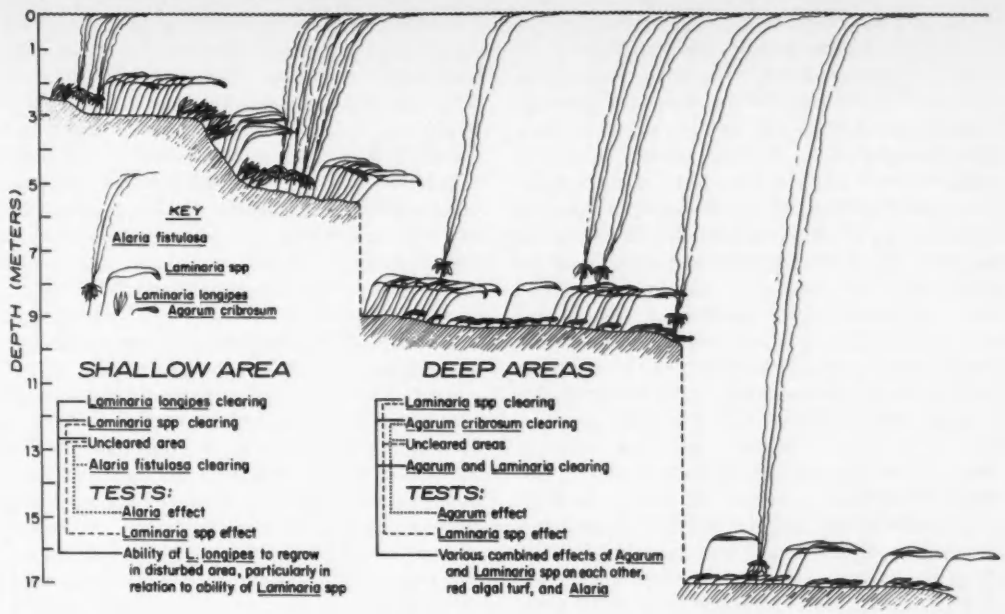

FIGURE 1.—Drawing of the kelp canopies at three different depths. *Laminaria* spp. refers to the large and very similar stipitate *L. groenlandica*, *L. dentigera*, and *L. yezoensis* which seem to occupy broadly overlapping depth profiles but form identical canopies because the stipe lengths and frond sizes are very similar. Diagrams of the experimental design testing hypotheses about the competitive effects between canopies is included for the two manipulated areas.

about the competitive effects these canopies have on each other, the role of physical disturbance in canopy composition, and a gradient of herbivore pressures in deeper waters, where the sea otter foraging becomes less efficient.

METHODS

This research was done in July 1971 and April 1972 in a small bay between the remains of the old Constantine jetty and Kirilof Point on the Bering Sea. A total of 34 dives were made during the study. There were two study sites, a nearshore shallow (< 5 m) area beside an old quarry and a deeper (>7 m) reef about 150 m offshore. Immediately offshore in the shallow area there is a very heavy summer canopy of *Alaria* mixed with a dense growth of annual brown algae such as *Cymathere triplicata* (P. et R.) J. Ag., *Desmarestia intermedia* P. et R., and numerous species of red algae representing such genera as *Ptilota*, *Hypophyllum*, etc. Offshore from this dense algal band, but still in the shallow area, are distinct patches of *Alaria* with thick canopies floating on the surface and patches of a very solid secondary *Laminaria* canopy. There are two *Laminaria* growth forms in the more shallow (< 5 m) area: *L. groenlandica*, *L. dentigera*, and *L. yezoensis* are solitary plants with one heavy 50-150 cm stipe per plant; *L. longipes* has thin multiple 20-40 cm stipes from a single rhizomelike holdfast (Markham 1968, 1972). The third prostrate canopy is represented in shallow water by scattered individuals of the heavy brown alga *Thalassiophyllum clathrus* (Gmelin) P. et R. The deeper offshore reef has a scattered and relatively thin (0-20%) canopy of *Alaria* and in the more shallow (7-12 m) levels a very thick canopy cover of *Laminaria* spp. With increasing depth the *Alaria* density decreases and the *Laminaria* is gradually replaced by *Agarum cribrosum* which forms the third prostrate canopy.

The experimental sites were chosen on the basis of distinct patches of the respective canopies to be manipulated and on the ease of shore access and relocation. Pruning shears were used to clear areas by cutting the stipes just above the holdfasts. In every case an immediately adjacent area was monitored as a control.

Methods of estimating percent canopy cover varied. The *Alaria* canopies represent visual estimates. The 100% covers were very thick and in these cases the floating stipes seemed to form an almost impenetrable wall in the water column. A few photographs taken of the *Alaria* canopy in areas where it had less than 100% cover suggest that the visual estimates in these locations were conservative. The other percent cover estimates were made with the aid of 0.25 or 0.16 m^2 quadrats which, in larger areas, were placed haphazardly, and in restricted experimental areas were placed systematically in such a way that the entire experimental area was sampled. The actual measurements were usually taken planimetrically from photographs as defined earlier (Dayton 1971). There were a number of cases in which visual estimates were used because of camera malfunction, running out of film, etc. I have compared such visual estimates with planimeter measurements and found that they are usually within 5% and always within 10% of each other (Dayton 1971, 1975). The data are presented as means because the actual sample numbers varied (but except where stated, were never fewer than 10); the variance is given as standard error.

RESULTS

Shallow Area

This area is covered with an extremely thick growth of algae and is generally characterized by a conspicuous absence of herbivores (Estes and Palmisano 1974). I was surprised to find sea urchins[2] among the *Laminaria* (especially *L. longipes*) haptera and holdfasts upon removing the canopies for the experiments discussed below. The sea urchins may exist in these sheltered refuges because the canopy is both very dense and relatively close (25-35 cm) to the substratum, thus seriously reducing the foraging efficiencies of their visual predators. This sea urchin-refuge hypothesis was supported by the observation that the sea urchins remained untouched in both clearings from 3 and 6 July through 8 July, but all were gone on 9 July. I suspect that they were taken by a sea otter that found the cleared patches, as one was observed foraging in the vicinity on the morning of 9 July. However, predation by the common eider, *Somateria mollissima* (Williamson and Emison 1969), and emigration are other possible explanations. At any rate, the small size (< 15 mm) and scarcity of these sea urchins do not seriously affect the contention that the herbivores have largely been eliminated from this area. The elimination of the grazing pressures makes the competition-based hypotheses discussed below more meaningful.

Hypothesis I

The *Alaria fistulosa* canopy excludes *Laminaria* spp. This hypothesis was tested (a) by cutting *Alaria* from several rocks and observing whether *Laminaria* recruited in the absence of *Alaria* and (b) by cutting *Laminaria* and observing potential *Alaria* recruitment. *Alaria* and probably *Laminaria* spp. were fertile at the time of the cutting. Significantly more *Laminaria* recruitment into *Alaria* clearings than into uncleared controls would support the hypothesis, whereas significantly more *Alaria* recruitment into *Laminaria* clearings than into the control would negate the hypothesis and suggest the truth of the converse hypothesis, that *Alaria* behaves as an opportunistic or fugitive species (Dayton 1973, 1975) in the presence of competition with the competitively dominant *Laminaria* spp. The results of such clearings at a depth of 5 m (done 3 and 4 July 1971) are presented in Table 1. The

[2]Opinions are divided whether the Amchitka sea urchin is *Strongylocentrotus drobachiensis* or *S. polyacanthus*.

TABLE 1.—Effects of canopies of *Alaria fistulosa* and *Laminaria* spp. on each other and on the cover of red algae in the nearshore experimental area (25 m^2) at 3-5 m depth. The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean. Data presented without variance were visual estimates. Control no. 1 suffered heavy algal loss from winter storms. The mean density of *A. fistulosa* in the April 1972 *Laminaria* removal experiment was 14.7 (± 1.1, SE) in ten 100 cm^2 quadrats.

	Alaria removal		*Laminaria* removal		Control no. 1		Control no. 2	
Canopy species	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Alaria fistulosa	[1]75	20.3 ± 20.0	5	100	45	100	10	5
Laminaria spp.	35.7 ± 15.0	39.2 ± 12.1	[1]87.2 ± 7.9	0	[2]100 ± 0	25.3 ± 20.0	100 ± 0	100 ± 0
Red algal turf	40.4 ± 10.7	45.6 ± 13.6	15.3 ± 8.6	45.5 ± 4.6	10.2 ± 5.8	40.2 ± 12.0	5.4 ± 5.3	15.8 ± 7.9

[1]Signifies that the canopy was experimentally removed.
[2]Canopy ripped out during winter storms.

Alaria forming a 75% canopy were removed from a 25 m^2 area and no significant change was observed in the *Laminaria* or red algal turf canopies by April 1972. But the removal of an 87% cover of *Laminaria* produced dramatic (5-100%) increases in the *Alaria* cover and a significant ($P<0.001$) increase in the red algal turf covers (*t*-test run on data normalized with an arcsine transformation). The 100% *Laminaria* cover in Control no. 1 suffered heavy damage when two large boulders, rolled about by winter storms, reduced *Laminaria* densities and resulted in significant increases in recruitment of *Alaria* and red algal turf covers ($P<0.01$). In addition to the extremely heavy *Alaria* recruitment in the *Laminaria* removal areas, there were also patches of *Rhodymenia palmata* (L.) Greville, *Ptilota* spp., *Desmarestia* spp., *Cymathere triplicata*, *Chaetomorpha melagonium* (Weber et Mohr) Jutz., and *Coilodesme* spp. No significant changes were observed in Control no. 2. To a certain extent these observations could be explained by a very slow growth rate of *Laminaria* spp. But certainly the hypothesis that *Alaria* dominates in competition over *Laminaria* was negated, and these data strongly support the conclusion that despite the expected competitive advantage gained by forming a surface canopy, *Alaria fistulosa* is not a competitive dominant, but a fugitive species colonizing areas released from competition with the dominant *Laminaria* canopy.

Hypothesis II

The rhizoidal growth pattern of *Laminaria longipes* allows an efficient recovery following a disturbance (Markham 1968). The hypothesis suggests that the removal of an *L. longipes* canopy results in the area being succeeded by its own extensive vegetative regrowth, in contrast to the invasion of many individuals of fugitive species seen following the removal of a mixed species canopy of *Laminaria groenlandica*, *L. yezoensis*, and *L. dentigera*. This hypothesis was tested by cutting the stipes near the holdfasts of a 100% cover of *L. longipes* from a 10 m^2 patch at a depth of 3 m on 7 July 1971. Fifteen ¼ m^2 quadrats observed after the 100% canopy was removed showed the following mean substratum covers: 57% (± 4.9, SE) *L. longipes* holdfasts, 7% (± 1.8, SE) sponges and compound tunicates, and 22% (± 5.2, SE) coralline algae, mainly *Clathromorphum* spp. They also showed mean ¼ m^2 densities of the sea urchin, *Strongylocentrotus* sp., of 17.5 (± 3.8, SE) and the asteroid, *Leptasterias aleutica*, of 1.0 (± 0.3, SE). Spores of the three other *Laminaria* species and of *Alaria* were potentially available from many plants on rocks on three sides of the clearing.

By April 1972, the clearing had been completely recolonized by *L. longipes*, despite the proximity of large plants of the other species. The recovery was so complete that the clearing could only be recognized after a long search located a few "landmarks" (sponges, compound tunicates, and a *Laminaria yezoensis* holdfast with the stipe cut by pruning shears) photographed the previous year. This strongly supports the hypothesis that the rhizoidal growth pattern of *L. longipes* is an effective adaptation for the recovery of its canopy following a disturbance and is in marked contrast to the heavy *Alaria* recruitment following the removal of a nearby *Laminaria* spp. canopy. I was unable to test the obvious hypothesis that this capacity for vegetative growth gives *L. longipes* an advantage over the other *Laminaria* spp. in a disturbed area, but loses a competitive advantage in less disturbed areas because the other *Laminaria* species have a higher, more effective canopy.

Offshore Area

An exploratory dive was made on the deeper offshore reef to investigate the relationship between sea urchin densities and the various algal canopies. Samples were taken from haphazardly placed ¼ m^2 quadrats. Five samples taken in the 12-15 m range showed means of 44% (± 23.3, SE) cover of *Laminaria* spp. and 62% (± 15.7, SE) cover of *Agarum cribrosum*, and a mean density of 11.2 (± 3.8, SE) sea urchins per ¼ m^2. In the 15-21 m depth range five samples provided means of 36% (± 13.0, SE) canopy cover of *Laminaria* and 80% (± 4.9, SE) canopy cover of *Agarum* with a mean sea urchin density of 6.4 (± 3.2, SE) per ¼ m^2. Few identifiable foliose algae were seen below 21 m, but there was a high mean sea urchin density of 30.4 (± 3.7, SE) per ¼ m^2. In these deeper areas there was almost a complete substratum cover of the encrusting coralline algae *Clathromorphum* spp. and the green alga, *Codium ritteri*. Only four *Alaria* plants were encountered in these 17 samples; all were growing from the top portion of one Laminaria stipe at 11 m.

On 11 and 12 July 1971, a study site was chosen and the data in Figure 2 labelled July 1971 were collected. The differences between these data and those given in the preceding paragraph give an idea of the variation in this area. The inverse relationship between the percent cover of *Laminaria* and *Agarum*, in which the *Laminaria* decreases and the *Agarum* increases with depth and sea urchin density, suggests that in shallow water *Laminaria* competition suppresses the growth of *Agarum*, but that *Agarum*, which has been demonstrated to be highly distasteful to *Strongylocentrotus drobachiensis* (Vadas 1968), is more successful in the presence of a moderate density of grazers. Finally, *Agarum* itself may also have an important competitive effect against *Alaria* and the foliose red algal turf. Grazing pressure and limiting light conditions probably cause the severe reduction of foliose algae in deeper water. These data demonstrating high densities of sea urchins at depths below 20 m agree with the observations of Barr (1971), Estes and Smith (1973), and Estes and Palmisano (1974). This suggests that sea otters at Amchitka do not forage effectively below 18-20 m.

That the experimental area could not be continuously monitored meant that it was not possible to manipulate the sea urchin density, but competitive effects of the algae at this depth were readily testable by selective removal of algal species.

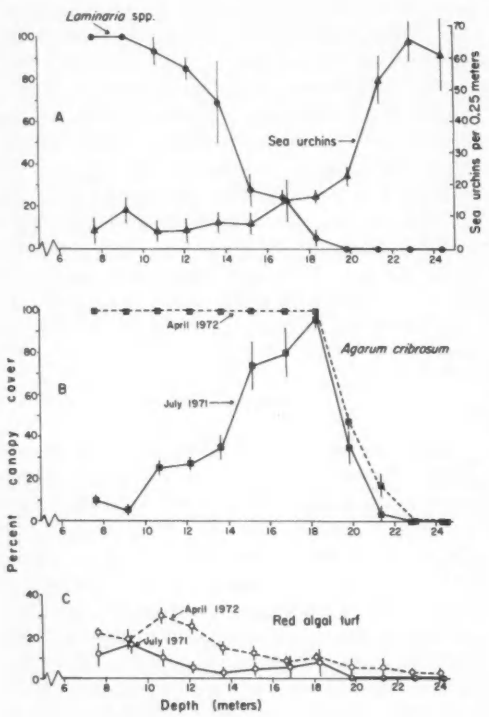

FIGURE 2.—Mean sea urchin densities and percent covers of *Laminaria*, *Agarum*, and red algal turf canopies at increasing depths before (July 1971) and after (April 1972) the *Laminaria* canopy was removed. Figure 2A contrasts the decreasing *Laminaria* cover with increasing sea urchin density in July 1971. Note that the *Agarum* canopy cover at that time shown in Figure 2B is nearly complete only at those depths at which there is reduced *Laminaria* coverage and relatively low sea urchin density. After removal of *Laminaria*, the *Agarum* canopy increased dramatically at the shallower depths. The increase of red algal cover after *Laminaria* removal is shown in Figure 2C. Variance is presented as the 95% confidence interval around the mean.

Hypothesis III

The presence of *Laminaria* spp. has no effect on other algae. This hypothesis was tested by removing a 2-m wide strip of *Laminaria* from the area where the data in Figure 2A were collected. The hypothesis was negated as both *Agarum* and the foliose red algae canopies significantly increased their covers (Figure 2B, C). The spectacular increase in the cover of the *Agarum* canopy certainly resulted partially from growth of the fronds; however, samples taken in April 1971 and repeated in July 1972 at approximately the same spots along the experimental *Laminaria* removal strip, showed that the mean *Agarum* density increased significantly from 4.1 ($\pm$ 0.6, SE; ten ¼ m^2 samples) plants to 15.6 plants per ¼ m^2 (was calculated from ten 1/16 m^2 samples with a mean of 3.9; $\pm$ 0.4 SE). The increase in canopy cover of the red algal turf was less spectacular, but a one-tailed Wilcoxon matched-pairs signed-ranks test of mean percent canopy cover at all depths considered shows a significant ($P<0.005$) general increase after the *Laminaria* were removed, this despite the fact that April may be early in the season for red algal growth. Thus the *Laminaria* canopy in the presence of an *Agarum* canopy has an important effect on other algal species.

Hypothesis IV

The *Agarum cribrosum* canopy alone has no effect on the other algae. This hypothesis was tested by clearing 45-85% covers of *Agarum* from 4 m^2

plots at 9.1- and 16.8-m depths in July 1971. In both cases a 100% canopy of *Laminaria* persisted throughout the experiment. A slight recovery of the *Agarum* population was observed the following April (Table 2), but no significant differences were observed in the numbers or percent cover of the other species. Thus there is, at present, no reason to negate the hypothesis.

Hypothesis V

The *Agarum cribrosum* canopy in the absence of the *Laminaria* canopy has an important effect on the other species of algae. This hypothesis was tested by removing both *Agarum* and *Laminaria* canopies from 4 m^2 plots at 9.1- and 16.8-m depths. These clearings were then compared to those in the adjacent *Laminaria*-only removal experiments at the same depths (Figure 2C). A strict interpretation of this comparison suggests that either a *Laminaria* or *Agarum* canopy or both is sufficient to prevent an increase of red algal turf cover because there is, at those two particular depths, no significant increase of red algal turf in either the *Laminaria*-only or *Agarum*-only removal experiments (Figure 2C, Table 2). This interpretation is equivocal, however, as Hypothesis III demonstrated a slight but significant *Laminaria* effect on the red algal turf. There is no equivocation regarding the effect of the combined *Laminaria* and *Agarum* canopies on the red algal turf which increased from 7 to 49% at 9.1 m and 1 to 38% at 16.8 m (Table 2). These are much more dramatic increases than were observed in the *Laminaria*-only removal areas and convincingly argue for a strong *Agarum* effect in the absence of *Laminaria*. Some of the red algae in this experiment were *Ptilota asplenoides* (Esper) C. Ag., *Laingia aleutica* Wynne, *Hypophyllum ruprechtianum* Zinova, *Constantinea rosa-marina* (Gmelin) P. et R., *Pantoneura juergensii* (J. Ag.) Kylin, *Cirrulicarpus gmelini* (Grunow) Tokida et Masaki, *Turnerella* sp., *Callophyllis flabellulata* Harvey, and *Nienburgia prolifera* Wynne.

The most impressive effect of the *Agarum* canopy in the absence of *Laminaria* was its inhibition of *Alaria* recruitment. In each of the two quadrats from which both *Laminaria* and *Agarum* were removed, the *Alaria* cover, consisting of a heavy recruitment of juvenile plants, increased from 0 to 100% canopy cover (Table 2). The *Alaria* response was particularly impressive because the dense *Alaria* recruitment completely filled, but was perfectly contained within, the *Agarum*-and-*Laminaria* removal patches. The mean density increased from 0 to 22.8 *Alaria* plants per 1/16 m^2 ($\pm$ 3.5, SE). In contrast to this result in the *Agarum*-and-*Laminaria* removal area, there was no *Alaria* recruitment in the rather extensive area from which *Laminaria* alone was removed (Figure 2). This result also contrasts sharply with those of the shallow *Laminaria* removal experiments (Table 1), in which no *Agarum* canopy level existed. An adjacent control was monitored for each experimental clearing; no changes were observed in any of the controls.

The above comparisons demonstrate that both the secondary *Laminaria* canopy and the tertiary *Agarum* canopy individually can significantly reduce the recruitment of *Alaria*, the species which forms the primary surface canopy. Further evidence of the intense competition in the deeper area where both understory canopies exist is provided by the observation that, of 100 *Alaria* plants surveyed, 79 were utilizing secondary substrata with their holdfasts attached high on *Laminaria* stipes (Figure 1).

TABLE 2.—Effects of *Agarum cribrosum* and combined *Agarum-Laminaria* spp. canopies on each other, red algal turf, and *Alaria fistulosa* at 9.1-m and 16.8-m depths in the offshore study site. Each experimental clearing area was 4 m^2. The data are presented as percent cover with the variance presented as the 95% confidence interval about the mean; data presented without variance are visual estimates.

	Depth: 9.1 m				Depth: 16.8 m			
	Agarum (only) removal		*Agarum* and *Laminaria* removal		*Agarum* (only) removal		*Agarum* and *Laminaria* removal	
Canopy species	July 71	April 72	July 71	April 72	July 71	April 72	July 71	April 72
Laminaria	100 ± 0	100 ± 0	[1]100 ± 0	0	100 ± 0	100 ± 0	[1]100 ± 0	0
Agarum	[1]65.3 ± 23.4	11.5 ± 10.2	[1]45.5 ± 16.1	25.8 ± 11.9	[1]85.2 ± 33.4	17.5 ± 7.1	[1]77.4 ± 12.7	11.5 ± 4.0
Red algal turf	11.5 ± 12.9	8.4 ± 10.7	7.0 ± 4.9	49.2 ± 14.0	2.1 ± 5.6	0	1.2 ± 4.0	37.5 ± 10.2
Alaria	0	0	0	100 ± 0	0	0	0	100 ± 0

[1]Signifies that the canopy was experimentally removed.

DISCUSSION

The pattern emerging from these and other (McLean 1962; Lowry and Pearse 1973; Estes and Palmisano 1974) studies of sea otter-dominated communities is that by consuming the populations of invertebrate herbivores, the sea otter has an extremely important role in maintaining the structure of shallow algal communities. In this study, high densities of sea urchins are found below 18-20 m, suggesting that this depth is the lower limit of effective sea otter foraging in this area. It is interesting to note that this depth is much more shallow than the 30-fathom profile speculated by Kenyon (1969). In addition, this seems to be a much more shallow limit to efficient foraging than is exhibited by the California population of sea otters, as I have seen evidence of their foraging to at least 30 m in the Carmel Bay region.

Strong competitive interactions between species of benthic algae appear well expressed in the shallow nearshore waters of the Aleutian Islands which have sea otters. The shallower (3-5 m) waters, subject to severe storm disturbance, are functionally dominated by *Laminaria* species. When the larger *Laminaria* spp. (*L. groenlandica*, *L. dentigera*, and *L. yezoensis*) are removed, either experimentally or by natural storm disturbance, their space is quickly utilized by *Alaria fistulosa*. In contrast, the rhizomelike holdfast with multiple meristems of *L. longipes* appears to be an effective adaptation to disturbance, as it allowed quick regrowth of stipes and fronds after their experimental removal. In deeper water (12-20 m), where there are many sea urchins, *Agarum cribrosum* is one of the dominant algal species. *Agarum*, however, loses in competition for light to solid canopies of *Laminaria* spp., which have erect stipes supporting their fronds above the nearly prostrate *Agarum*. When freed from *Laminaria* competition, *Agarum* significantly increases its cover and abundance. When both *Laminaria* and *Agarum* are removed, there is a bloom of red algal turf and of *Alaria fistulosa*. These tests of competition-based hypotheses are probably valid despite the various depth-related changes in the physical environment because each was compared to immediately adjacent controls.

It is interesting to note that despite having potentially long-lived individuals and the competitively superior adaptation of a floating canopy, *Alaria fistulosa* behaves as a fugitive species with its densest distribution in the highly disturbed immediate offshore area, occurring farther offshore only in areas where two understory canopy levels are removed or by growing on *Laminaria* stipes. This is surprising because quite the opposite situation seems to exist in the southern California kelp community, where *Macrocystis pyrifera* forms a heavy surface canopy which may inhibit the growth of the understory species (North and Shaeffer 1964; Dayton unpubl. data). Although *Alaria* was observed in depths of over 25 m, its lower distribution appears to be restricted primarily by sea urchin grazing.

Other research (Estes and Palmisano 1974; Palmisano in prep.) contrasts the nearshore and intertidal communities of Amchitka with nearby otter-free islands and convincingly demonstrates the powerful role the sea otters have in structuring the nearshore community. This paper has experimentally demonstrated competitive trends between different canopy guilds in an algal community which contains an unusually high number (four) of *Laminaria* species which have semirigid stipes. It is tempting to speculate an evolutionary hypothesis in which the sea otters reduce the herbivore pressure and thus allow a competitive differentiation of niches of these large stipitate kelps. Such hypothetical evolutionary thought has the common and serious flaw of ignoring the roles of extinct species, many of which may have left large and important "vacant niches" (such as those left by the mammal extinctions of the late Pleistocene discussed in Martin and Wright 1967). This problem is particularly acute in the Bering Sea, as Steller in 1751 (reference in Gard et al. 1972) reported the giant sea cow, *Hydrodamalis gigas* (Zimmermann 1780), eating algae in the nearshore and tidal beaches of the Komandorskiye Islands. The large populations reported by Steller and various Russian and German sailors of this huge (ca. 10 tons, Scheffer 1973) kelp-eating (Stejmeger 1936) sirenian surely had important consequences to the kelp populations that weaken any present day speculation of the evolutionary consequences of kelp competition. It may be reasonable, however, to pose the hypothesis that by consuming invertebrate herbivores, particularly sea urchins, the sea otter was indirectly responsible for the high productivity of large algae necessary to maintain the sea cow populations. Such an hypothesis is supported by the overlap of the otter

and sea cow populations in the Pleistocene (Jones 1967; Kenyon 1969; and Gard et al. 1972). This relationship is nicely diagrammed in Scheffer's (1973) touching story of the last day of the sea cow.

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PRODUCTION OF TWO PLANKTONIC CARNIVORES (CHAETOGNATH AND CTENOPHORE) IN SOUTH FLORIDA INSHORE WATERS[1]

M. R. REEVE AND L. D. BAKER[2]

ABSTRACT

Seasonal changes in biomass and production of two planktonic carnivores, *Sagitta hispida* Conant and *Mnemiopsis mccradyi* Mayer, were followed in a subtropical inshore marine environment. Production was estimated as the product of mean daily biomass (calculated from the sampled biomass and computed mortality rates) and daily growth rate. The latter was determined from laboratory culture experiments at three temperatures. Seasonal fluctuations of ctenophore biomass and production were much greater than those of chaetognaths. Mean daily production in milligram carbon per square meter was 2.00 and 4.80 for *Sagitta* in Card Sound and Biscayne Bay respectively, and 1.01 for *Mnemiopsis* in Biscayne Bay. The ctenophore was absent from Card Sound, possibly because the zooplankton standing crop was an order of magnitude lower than in Biscayne Bay (excluding ctenophores). Average production/biomass ratios were 0.31 for *Sagitta* and 0.12 for *Mnemiopsis*.

Most production data for zooplankton are restricted to the herbivorous copepods in temperate and cold waters (see review of Mullin 1969; Mullin and Brooks 1970; Riley 1972). Estimates for carnivores are very few and include *Sagitta elegans* (McLaren 1969; Zo 1969; Sameoto 1971) and *Pleurobrachia bachei* (Hirota 1974).

As pointed out by Mullin (1969) there is no simple technique for the measurement of production of natural populations of zooplankton comparable to the relatively routine ^{14}C uptake method for the determination of primary production by phytoplankton. Unlike the phytoplankton, which share a common characteristic of a single trophic level, zooplankton extend over at least two trophic levels, and an individual species may vary its trophic status on the basis of food availability or life history stage. In addition, zooplankton range in size from 20 μm or less to 20 cm or more and have widely differing growth and reproduction rates. Attempts to measure total zooplankton production have been made, especially where a single species dominates the population over a period (e.g., Cushing and Vucetic 1963) or where a single group (such as copepods) dominates and is treated as a unit (e.g., Riley 1972), and most recently by relating respiration to temperature and body weight and applying these data to the plankton biomass of the Kuroshio (Ikeda and Motoda in press).

The data reported below are based on the individual species approach, using experimentally determined growth rates to compute production from environmental biomass estimates for two planktonic carnivores, widely separated phylogenetically but dependent upon the same source of food.

STUDY SITE AND SAMPLING METHODS

The study area consisted of Biscayne Bay and Card Sound which form part of an extensive system of shallow, warm, semiestuarine, and semienclosed interconnected water bodies typical of the coastal region of a large part of Florida. Zooplankton sampling programs were conducted at 4 stations on 28 dates throughout 1971 in Card Sound and at 11 stations on 26 dates from October 1970 to February 1972 in central Biscayne Bay. Detailed reports of these programs were given by Reeve and Cosper (1973) and Baker (1973), respectively.

In both locations, surface tows were made with a metered, ½-m mouth diameter net of 200-μm mesh. In addition, a similar net of 64-μm mesh was used in Card Sound. In Biscayne Bay, a 1-m, 705-μm mesh net with a 14-liter flexible, vinyl cod end was employed to collect ctenophores. It was not used routinely in Card Sound because ctenophores

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were not encountered. Zooplankton were thus collected from both locations using two nets (which were towed simultaneously), one of which (the 200-μm mesh) was common to both locations.

An extensive series of samples was collected in Card Sound to check on the adequacy of the 64- and 200-μm mesh ½-m mouth diameter nets in sampling the entire size range of the population of *Sagitta hispida*. In comparisons between a 64- and 35-μm mesh, the size-frequency distribution of the population was not significantly different. Absolute numbers often differed, but this was attributable to the rapid clogging of 35-μm mesh, which rendered flowmeter readings unreliable, and was why this mesh was not used routinely. The 64-μm mesh net, which filtered less than 50% of the volume of water of the 200-μm mesh in the same time, collected fewer of the larger size chaetognaths than the 200-μm mesh, indicating that a greater proportion of the larger animals were avoiding the smaller meshed net. Comparative tests between the 200-μm ½-m diameter net and a 200-μm 1-m net (which filtered 3 times more water) did not indicate that the larger net caught either a larger absolute number, or a higher percentage, of the larger size classes per volume filtered. These data are available by writing to the first author. It appeared, therefore, that the two standard ½-m nets utilized in the sampling program quantitatively collected the entire size range of this species in the surface water.

Vertical distribution of *S. hispida* Conant in the 3-m water column was investigated on six dates during the year using both towed nets and a pump as described by Reeve and Cosper (1973). There was considerable variability in vertical distribution between sampling dates, due in part to variability in incident radiation and water turbidity, but it was estimated that the numbers per cubic meter from surface hauls should be multiplied by a factor of 1.54 to obtain a mean water column density per cubic meter in the 3-m deep water column. This factor was very close to the 1.45 calculated for the plankton as a whole, by Reeve and Cosper (1973). As noted previously (Reeve and Walter 1972), *S. hispida* has the ability to attach itself to substrates in the laboratory and lays its eggs on surfaces in clumps. It does not attach significantly until near maturity and even then, most of the population is usually to be found swimming in the water column in aquaria. We believe that the biomass estimates of our plankton samples were not biassed downwards due to this behavioral pattern, as eggs are usually laid at night while the plankton samples were taken during the day, and the vertical sample series gave no indication of a higher proportion of older animals nearer the bottom. On the other hand, comparisons of the size-frequency distribution of a population sampled with a towed net and with an Okelmann sledge lightly skimmed across the bottom, which is an effective means of sampling the benthic *Spadella*, usually yielded a few mature individuals in the larger size classes which were absent from the net. The sledge, however, only provided a qualitative sample and it was not possible to adjust the biomass of Table 1 to take these few animals into account. Our biomass estimates are, therefore, slightly underestimated on this account. No estimates of egg numbers were made, since *Sagitta hispida* does not deposit them in the water column, but attaches them to objects on the bottom.

Ctenophores presented different sampling problems. Lobate ctenophores, such as the genus *Mnemiopsis*, tend to break up easily in nets and are rapidly disintegrated in the usual fixatives. Baker (1973) reported that transference of individual, newly hatched larvae by pipette from one beaker to another would result in the disappearance without a trace of over 90% of these 200-μm diameter animals. It was futile, therefore, to attempt to assess the numbers of eggs or the smallest larvae from net tows, and probably some of size class A (0.8-4.4 mm) were also fragmented beyond recognition. Even so, the pattern of distribution of biomass between the size classes (Table 1) suggests that the fraction contributed by the smallest unsampled or inadequately sampled members of the population is small. It may be presumed that animals in the larger size classes were not avoiding nets, since *Mnemiopsis* is a weak swimmer with no rapid escape behavior, and hence were sampled adequately. No feasible method was devised of making tows near the bottom of this shallow water column with a 1-m mouth diameter net, and pumps were impractical for sampling ctenophores. The only indication we have that *Mnemiopsis* does not exhibit any marked vertical layering are observations by scuba.

Analysis of Samples

The chaetognaths of the preserved samples (all of which belonged to the species *S. hispida*) were

TABLE 1.—Summary of biomass and production data for *Sagitta* and *Mnemiopsis* by size class averaged over the entire survey period.

	Sagitta Size class (live length)									*Mnemiopsis* Size class (live volume)				
	A <2.5	B 2.5–3.7	C 3.8–4.9	D 5.0–6.2	E 6.3–7.4	F 7.5–8.7	G 8.8–9.9	H 10.0–11.3		A 0.0021	B 0.052	C 0.92	D 15.0	E 28.0
Numbers per cubic meter	87.4	66.0	33.3	13.7	3.32	0.40	0.031	0.008		2.90	1.50	0.225	0.157	0.075
Mean duration (days)	12	4.7	2.8	2.7	1.7	2.0	5.5	9		8.7	2.0	17	10	16
Ash-free dry weight per organism (μg)	2.18	10.1	29.5	71.2	132	218	349	531		19.7	507	12,100	140,000	278,000
Ash-free dry weight per size class (μg/m³)	191	667	982	975	438	87.2	10.8	4.2		57.0	761	2,730	22,000	20,900
Daily net production (μg ash-free dry wt./m³)	72.5	244	289	290	63.1	13.1	0.78	0.17		60.9	452	936	1,800	1,860
P/B	.38	.37	.29	.30	0.14	0.15	0.07	0.04		1.1	0.59	0.34	0.08	0.09
Growth	0.25	0.25	0.25	0.25	0.25	0.25	0.083	0.044		0.50	0.50	0.21	0.069	0.069
Coefficient	0.35	0.35	0.35	0.35	0.35	0.35	0.074	0.007		0.78	0.78	0.23	0.071	0.071
	0.41	0.41	0.41	0.41	0.41	0.11	0.041			0.65	0.65	0.23	0.069	0.069
								0.3						
										<0.01		1.8	<0.01	0.08
Mortality	21	<0.01	0.04	0.15	0.40	0.85			1.5	<0.01		1.1	0.03	0.07
Coefficient	26	<0.01	<0.01	0.55	0.30	3.5			2.0	<0.01		0.76	0.05	0.09
	31	<0.01	0.30	0.90	2.0	4.0								

counted and measured in the laboratory. The Card Sound samples from the four stations were pooled for each net on each sampling date in proportion to the filtered volumes they represented (Reeve and Cosper 1973). Aliquots of each pooled sample were taken such that they contained between 50 and 100 organisms. The total body length of each animal was measured (see Reeve 1970). The entire sample was examined for mature animals. The lengths were tabulated in 1-mm preserved length size classes (see next section for conversion to live length). Since two values were obtained for each size class from the Card Sound samples (i.e., one for each mesh size) the larger number was taken as the correct one, on the assumption that the smaller value was due either to avoidance by larger animals of the 64-μm mesh, or escape of the smaller animals through the 200-μm mesh.

The pooled 200-μm Biscayne Bay samples were treated similarly. The numbers of *S. hispida* in Biscayne Bay were estimated by adjusting the numbers in each size class in the 200-μm net to total number on the basis of ratios computed for the 64- and 200-μm counts from Card Sound.

Analysis of ctenophore samples from the 1-m net presented special difficulties, because there was no known satisfactory method of preservation of lobate ctenophores. Following Miller (1970) analysis was performed on deck immediately after recovery of the net (see Baker 1973). The contents of the cod end were emptied into a stack of wire sieves of arbitrarily chosen decreasing mesh sizes (25-, 12.5-, 6.25-, 3.0-, and 0.7-mm mesh openings) immersed in seawater. The ctenophores from each sieve, except the smallest, were transferred to a graduated cylinder and the total volume of organisms retained by each sieve measured. The average volume per individual retained in each sieve was determined either by counting the total number of animals in each sieve or, in the case of the larger animals, by direct volume displacement of randomly selected individual ctenophores. It was impractical to follow this routine with the smallest animals (0.7-mm sieve) since their total volume was too small to be measured accurately. Instead, they were resuspended in seawater, transferred to plastic bags, and returned to the laboratory where they were counted. No attempt was made to assess the number and hence production of ctenophores smaller than 0.7 mm in diameter.

Conversion of Raw Data to Other Units

The shrinkage in length of *S. hispida* with Formalin[3] preservation was estimated by measuring over 100 live animals from a freshly caught 200-μm mesh sample, and repeating this 10 and 420 days following preservation of that collection in a 5% formaldehyde solution buffered with methenamine, which was the standard preservative for all plankton samples. The degree of shrinkage was judged by the extent of the downward shift in the peak of the length/frequency histogram. Half the total shrinkage (12.5% of the original length) occurred within the first 10 days. Assuming a linear rate of shrinkage after day 10, and preservation time of the samples before analysis varying from 1 to 9 mo, the degree of shrinkage was computed to be 20% with a range of ± 3.5%. This mean estimate was used to adjust size classes from preserved to live length.

Live length was converted to dry weight using the relationship obtained from a linear regression analysis of more than 40 separate weight determinations of animals over their entire size range. Animals to be weighed were rinsed in isotonic ammonium formate and dried at 60°C. The ash-free (i.e., organic) dry weight was previously determined to be 90.7% of the dry weight (Reeve et al. 1970). The mean carbon and nitrogen content of *S. hispida* was determined by a Perkin-Elmer elemental analyzer to be 44.9% with a standard error of ± 1.0% and 11.9% ± 0.2% of the ash-free dry weight from 23 separate estimations over its entire size range. The raw biomass units for ctenophores were obtained in terms of live volume. Over 100 separate determinations of animals over their entire size range were made for wet (drained), dry (at 60°C), and ash (at 500°C) weights. Live volume was approximately numerically equal to wet weight (1.000 ml = 0.958 ± 0.002 g standard error). Dry weight was 4.43% ± 0.40% of wet weight and ash-free dry weight was 21.90% ± 0.15% of dry weight.

Eighteen separate determinations of carbon and nitrogen content of *Mnemiopsis mccradyi* Mayer were made which yielded unusually low values 8.72% ± 0.06% and 2.32% ± 0.07% of the ash-free dry weight of carbon and nitrogen respectively. A value of 44.9% carbon was reported for *Sagitta* (above), and Curl (1962) quoted values for various planktonic crustaceans between 44 and 52%. Even his value for *Mnemiopsis* sp. was considerably higher at 20.6%. Hirota (1974) assumed a 50% carbon content of organic weight for *Pleurobrachia bachei* in his calculations, because analysis by wet combustion with acid dichromate was unsuccessful due to problems with chloride ion interference (J. Hirota, pers. commun.).

We considered the possibility that our analyses were also yielding incorrect results and tested three possible sources of error: a) interference in the analysis by the unusually large amount of inorganic salts present in the ctenophore tissue, b) errors of dry weight determination, and c) errors of ash weight determination. Mixtures of bovine serum albumin (5-15%) and sodium chloride did not reduce the theoretical yield of carbon when combusted in the elemental analyzer. Since, however, the dried ctenophore material was a more intimately bound complex of organic and inorganic substances, which might be more resistant to complete combustion, potassium persulfate was added to promote complete oxidization (see Strickland and Parsons 1968). No increase in carbon yield was achieved by this method. The reliability of dry and ash weight determinations affects the reliability of the carbon value since the numbers so obtained are used in its computation. The possibility of any significant loss of organic matter during drying at 60°C was checked by performing carbon analyses on freeze-dried material. The previously derived mean value remained unchanged. Finally, ash weights were determined at a temperature 100°C lower than previously. Slightly higher ash weights resulted, which in turn slightly increased the computed carbon level to 10.3% of the ash-free dry weight. Since any significant source of error in this determination has so far eluded us, we report production values below for ctenophores and chaetognaths in terms of ash-free dry weight for direct comparison and in terms of the analyzed carbon. Mullin (pers. commun.), on the basis of unpublished observations, suggested that the weight lost on ashing may be largely "bound" water, and that in *Pleurobrachia bachei*, at least, only about 12% of the ash-free dry weight is organic matter. This suggests that comparisons based on carbon content are more valid than those based on "organic" or ash free-dry weight.

Growth Rates

Growth rates of populations of the ctenophore

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and chaetognath were determined in the laboratory using larvae hatched from wild adults according to methods detailed by Reeve and Walter (1972) for *S. hispida* and Baker and Reeve (1974) for *M. mccradyi*. Three separate populations of the chaetognath and two of the ctenophore were grown at each of three temperatures (21°, 26°, 31°C), which corresponded to the mean monthly minimum, annual mean, and mean monthly maximum temperatures (to the nearest 1°C) off the laboratory dock in Biscayne Bay over 11 yr (unpubl. records). Food was provided in the form of naturally occurring zooplankton of suitable size (see previously cited information on culture technique), consisting mostly of the copepods *Acartia tonsa* and *Paracalanus parvus*, maintained at a level such that no more than 50% were grazed down over 24 h.

Growth rates were measured as length increase to avoid sacrificing any members of the populations and the data converted to ash-free dry weight as previously described. Total length of *Mnemiopsis* was measured from the aboral to the oral pole (or tip of the oral lobes in adults) as described in detail by Baker (1973).

Production Calculation

The method of calculating production was that employed by Mullin and Brooks (1970) and Hirota (1974), where for each size class an exponential coefficient of daily growth (G) and mortality (M) is obtained from laboratory growth rate and field size-frequency data.

The growth coefficients were computed from the slope of the line relating the logarithm of increase in ash-free dry weight and age (Figure 1) following Crisp (1971). Data from each rearing experiment were combined for each species at the specified temperature. For *S. hispida*, the semilogarithmic relationship is linear over most of its size range until growth levels off at maturity (Reeve and Walter 1972). The termination of the linear (i.e., constant exponential growth) phase was arbitrarily set at 20, 25, and 30 days at 31°, 26°, and 21°C respectively, and the slope of the line calculated by linear regression analysis. At each temperature, slopes at two points beyond the linear phase were required, and these were derived by extrapolation on the basis of the remaining data points and other (unpubl.) data on lengths of

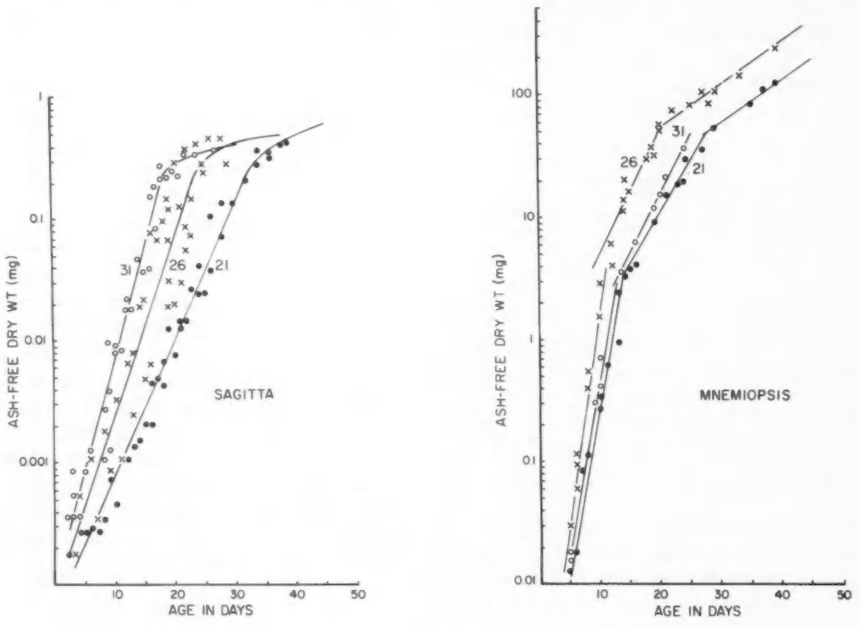

FIGURE 1.—Growth rate of *Sagitta* and *Mnemiopsis* at three different temperatures.

animals older than those surviving in these experiments. The potential errors in such a procedure are minimal, because the coefficients are tending towards zero and the biomass involved in the two largest size classes is only a small percentage of the total.

The *Mnemiopsis* growth curves were treated differently because their slopes decreased progressively with age. In order to facilitate computation of the required slopes, the curves were divided into segments, the junctions of which were assigned by visual inspection to be at 3- and 50-mg ash-free dry weight. The slopes of the individual segments A, B, and C were individually calculated from the population mean points within them by linear regression analysis. Unlike *S. hispida*, where growth rate is proportional to temperature between 21° and 31°C, *M. mccradyi* grows faster at 26°C than at either end of the range. Survival was poor at 31°C, populations dying out by the 25th day. Since no points exist from which to compute a slope for segment C at 31°C, it was taken to be the same as that for the 21°C experiments, since segments A and B at the two temperatures are almost identical.

Sampling dates were divided into three groups on the basis of the proximity of the ambient water temperature to 21°, 26°, and 31°C so that growth coefficients derived for these temperatures could be applied to the standing stock data. Similarly, mean mortality coefficients were derived for the three temperature ranges by averaging the numbers of animals in each size class over the sampling dates in each temperature range. These mean numbers were used to obtain mean ratios of Y/X (as did Mullin and Brooks 1970) where X and Y are the numbers of the earlier and later of two successive size classes. This ratio, and the duration of development in each of the two successive size classes, enables calculation of the exponential coefficient of daily mortality between the two size classes using computer-generated tables. We recognize that this procedure is an approximation which probably oversimplifies actual conditions by making unproven assumptions regarding constancy of mortality rate with time and between adjacent size classes, yielding a single value for m rather than a measure of its possible range (see Fager 1973).

The duration of development in each size class at each temperature range was estimated from the arbitrarily defined limits of each size class and the laboratory growth rate data.

Net production of a size class on a given sampling date, taking into account animals which die before the end of the day, is the product of the mean biomass and the daily exponential coefficient of growth for that temperature range. The day is assumed to start at the time of sampling, and the mean biomass ($\overline{WN}$) of that size class over the subsequent 24 h is obtained by application of the relationship given by Mullin and Brooks (1970) which utilizes the initial biomass, growth, and mortality coefficients. The initial biomass (WN in ash-free dry weight) is the product of sampled numbers (N) and mean ash-free dry weight (W) of an individual organism of that size class. Summing the production values for each size class provides an estimate of the total net production of the population on that day. No attempt was made to estimate egg production in either species.

Net production was determined for chaetognaths of the Card Sound population only; values quoted below for the Biscayne Bay population are estimated by applying the mean population production/biomass ratio for Card Sound to estimated total biomass in Biscayne Bay. An estimate of annual production is obtained by taking each sampling date as the midpoint of each sampling period, summing the product of daily production and number of days in that sampling period, and summing the total production for each sampling period and adjusting for 365 days. In the ctenophore population, which was sampled for 17 mo, and passed through two biomass peaks which Baker (1973) considered to be an annual winter event (Table 2), two values were computed (see Table 3), one for 365 days from the beginning and one for 365 days up to the end of the sampling program.

Results and Discussion

Seasonal Changes

Summaries of the population dynamics and production data are contained in Tables 1 and 2, computed as detailed above from tabulations by sampling date and size class. Figure 1 contains the laboratory growth rate data. The standing stock and production data are summarized in Tables 1 and 2, and are derived from the Card Sound population of *Sagitta* and the Biscayne Bay population of *Mnemiopsis*, since these populations had been the most effectively sampled. For each size class (Table 1) averaged over the entire

TABLE 2.–Summary of biomass and production data by sampling data averaged over all size classes.

Sagitta				*Mnemiopsis*			
Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B	Date	Biomass mg ash-free dry wt/m³	Production mg ash-free dry wt/m³/day	P/B
1/06/71	3.82	0.95	.25	10/12/70	18.02	2.64	.15
1/23/71	2.86	0.62	.22	10/23/70	135.59	12.12	.09
2/06/71	2.94	0.74	.25	11/20/70	314.31	27.80	.09
2/16/71	7.09	1.44	.20	12/15/70	81.97	6.92	.09
3/05/71	3.68	0.94	.26	1/15/71	18.31	2.09	.11
3/19/71	1.56	0.40	.26	2/15/71	23.56	2.35	.10
4/02/71	4.89	1.28	.26	3/12/71	5.46	0.67	.12
4/16/71	4.10	0.96	.23	4/08/71	20.34	1.63	.08
4/30/71	11.98	3.11	.26	5/07/71	17.77	1.49	.08
5/14/71	5.53	1.77	.32	6/03/71	0.22	0.04	.18
5/28/71	2.50	0.69	.28	7/01/71	0.87	0.12	.14
6/11/71	4.46	1.54	.35	7/26/71	0.17	0.01	.06
6/25/71	1.24	0.46	.37	8/25/71	–	–	–
7/09/71	1.58	0.60	.38	9/17/71	0.06	<0.01	.06
7/23/71	0.10	0.04	.40	9/30/71	0.58	0.09	.16
8/06/71	0.56	0.23	.41	10/14/71	1.29	0.14	.11
8/20/71	0.25	0.10	.40	10/28/71	3.27	0.64	.20
9/03/71	0.48	0.19	.40	11/12/71	8.86	1.30	.15
9/09/71	0.62	0.24	.39	11/24/71	6.80	1.07	.16
9/14/71	6.03	2.26	.37	12/02/71	56.55	6.14	.11
9/21/71	2.00	0.66	.33	12/20/71	20.89	2.16	.10
9/28/71	3.47	1.24	.36	1/06/72	200.35	15.66	.08
10/14/71	4.85	1.67	.34	1/21/72	103.59	7.38	.07
10/26/71	6.06	2.23	.37	2/03/72	7.69	0.75	.10
11/09/71	0.99	0.37	.37				
11/23/71	3.93	0.97	.25				
12/07/71	5.21	1.27	.23				
12/15/71	1.16	0.30	.26				

sampling period, the mean numbers, live length (or volume for *Mnemiopsis*), ash-free dry weight per organism, and ash-free dry weight per size class are tabulated. The mean net daily production of each size class (per cubic meter) averaged over the entire period using the information on daily rates of growth and mortality and the average duration of each size class (over the three temperatures) is also provided.

Seasonal changes in production reflected those of biomass generally as indicated in the production/biomass ratios (Table 2), which varied between 0.20 and 0.41 (mean, 0.31) for *Sagitta* and 0.059 and 0.20 (mean, 0.12) for *Mnemiopsis*. The ratios were highest in *Sagitta* in the summer when growth rates were maximum, but biomass and production was at its lowest. In *Mnemiopsis*, which also exhibited minimum summer biomass and production levels, the ratio tended to be low relatively, as was growth rate. This summer low point of biomass and production is a confirmation of the experience of some nine seasons of observation by the first author and is characteristic of the 200-μm net plankton of Card Sound and Biscayne Bay as a whole (for a discussion of which, see reviews of Reeve and Cosper 1973 and Reeve in press).

Throughout the rest of the year the chaetognath biomass of Card Sound and Biscayne Bay fluctuated much less widely than that of the ctenophores in Biscayne Bay. The biomass of *Sagitta* ranged (excluding July-September) between 1- and 12-mg ash-free dry wt/m³ in Card Sound and an estimated 2- and 20-mg ash-free dry weight in Biscayne Bay, whereas for ctenophores the range was 0.2 to 314 mg/m³. The mean annual biomass of *Sagitta* in Card Sound and Biscayne Bay was 3.36- and 8.04-mg ash-free dry wt/m³ and for *Mnemiopsis* in Biscayne Bay was 25.2- to 42.5-mg ash-free dry wt/m³ (reckoning 12 mo from the date of the first sample or 12 mo prior to the date of the last sample).

The range of net daily production rate in terms of ash-free dry weight for *Sagitta* at the surface from Card Sound and *Mnemiopsis* from Biscayne Bay was 0.04 to 3.1 and < 0.01 to 27.8/m³, respectively. Table 3 contains production estimates on an annual basis computed for surface and average water column (for *Sagitta* only) as ash-free dry weight and carbon per cubic meter. For *Mnemiopsis*, carbon production is computed both on the basis of the carbon content of *Sagitta* and the experimentally determined carbon content for *Mnemiopsis*. Daily production estimates per cubic meter and per square meter are also computed in terms of experimentally determined carbon content. As noted above, the two values in each case for *Mnemiopsis* incorporate successive annual production peaks.

TABLE 3.—Mean annual and daily production of the *Sagitta* populations of Card Sound and Biscayne Bay and *Mnemiopsis* population of Biscayne Bay.

	Annual production					
	mg ash-free dry wt/m³		mgC/m³		Daily production	
	Surface	Average water column	Carbon 44.9%	Carbon by analysis	mgC/m²	mgC/m²
Sagitta						
Card Sound	357	542	244	244	0.67	2.00
Biscayne Bay	855	1,200	584	584	1.60	4.80
Mnemiopsis						
Biscayne Bay	695/1,409		312/633	60.6/123	0.17/0.34	0.50/1.01

Details of methods for the calculation of production for populations with continuous breeding occur in Winberg (1971) and Crisp (1971). They are essentially similar to the method used here and by Mullin and Brooks (1970) and Hirota (1974) except that no adjustment is made to the sampled biomass (WN) to compute the mean biomass ($\overline{WN}$) during the 24 h immediately following the taking of the sample. This additional step, which we also performed, requires considerable extra effort (depending on the number of size classes and sampling dates involved) as well as access to computer services. In these warm waters, however, where growth and mortality rates may be less variable than in regions of more pronounced seasonality, the increase in W tends to cancel out the decrease in N, the difference between WN and $\overline{WN}$ for *Sagitta* and *Mnemiopsis* being less than 10% (93 and 108%, respectively).

Mortality coefficients tended to increase progressively with age in *Sagitta* and with increasing temperature. These environmental observations correspond to the conditions of laboratory cultures with respect to temperature, but in cultures young animals tend to die off more rapidly than juveniles and immature animals (Reeve and Walter 1972). A variety of interacting factors, including differences in predation pressure and food adequacy, may be responsible. In the ctenophore population the pattern of mortality is uniformally low except in size class B which corresponds to the time of change from tentaculate larva to lobate adult. The unmeasurable mortality of size group A can be partly attributed to sampling inefficiency, though this was shown not to be the case for *Sagitta* (see above).

Problems of Measuring Growth Rate

In animals such as copepods, with life history stages marked by recognizable and abrupt changes (i.e., molts), division of the cycle into parts may be accomplished on the basis of some biologically meaningful criteria. Both chaetognaths and ctenophores exhibit more gradual transformation from newly hatched larva to mature adult, and size class separation is based on arbitrary limitations such as preserved length or sieve size. The only real validity of the particular size classes used here is that they represent a progression from the youngest to the oldest animals. Factors such as variability of size of animals of the same age at different temperatures and imprecision of raw measurements (larger ctenophores may pass through a mesh slightly smaller than their diameter by their own weight deforming their shape) tend to blur the sharpness of the line separating one size class from the next. The arbitrary choice of size classes resulted in large variations in the durations of development of each size class. In *Sagitta* the mean duration (i.e., averaged over the three experimental temperatures) of the initial size class was 12 days, shortening to 2 days as length increased rapidly, and increasing to 9 in the last size class as a final length was approached in the adult. In *Mnemiopsis* size class durations proved to be even more erratic (see Table 1).

On the basis of the definitions used by Reeve (1970) for *S. hispida*, the larval, juvenile, immature, and mature stages correspond approximately to size classes A and B, C and D, E and F, and G and H, respectively. For *M. mccradyi* the tentaculate larva extends to size class C and the first eggs are also produced by size class C animals (29 mm and larger).

The most satisfactory way to determine growth and mortality in a population is to follow the increase in size and decrease in numbers of a cohort of the population over successive sampling dates by inspection of size-frequency histograms (Winberg 1971; Crisp 1971). In warmer waters, although biomass may fluctuate widely, breeding

tends to extend over most or all of the year and distinct cohorts can rarely be identified.

Growth rate, therefore, was measured in the laboratory, and in as large a volume as practical (30-70 liters). No attempt was made to simulate natural food levels. There were various reasons for this. Mean annual zooplankton concentrations of the 200-μm mesh, which is the food source of older *Sagitta* and *Mnemiopsis* (Reeve and Walter 1972; Baker 1973), were of the order of magnitude of 1 organism/liter, an impractically low concentration to work with in these volumes. It is certain that any environmental concentration estimated from a net tow is an average of several small-scale patches of higher and lower density. We have some information from direct observation by scuba (unpubl. data) that patch densities at least an order of magnitude greater occur, as well as information (also unpubl. data) that both *Sagitta* and *Mnemiopsis* can ingest food several times faster following a period of starvation than they do under conditions of a constant supply of food. *Sagitta* is capable, under certain conditions, of ingesting within 1 to 2 min all the food it consumes in 24 h under conditions of continuous abundant food supply.

Despite the fact that feeding habits and environmental food concentrations are poorly understood at present, it is clear that for carnivorous zooplankton, at least, maintaining a continuous supply of food at mean environmental concentrations in small-scale experimental conditions, would be as artificial as maintaining a continuous abundant supply, even though there must obviously be a relationship between total food supply and production in the environment. The latter method does provide a standard (i.e., maximum) growth rate. When better data become available on the interrelationships of feeding, food supply, and growth rate, the production estimates computed on that basis can be revised downward. At present, there is little information available to even guess to what extent these growth rates and hence production estimates are overestimations. Hirota (1974) reported surprisingly little difference in growth rates of *Pleurobrachia* in experiments at food concentrations ranging between 1 and 350 μgC/liter, but pointed out that in the 70-m^3 tank in which the low food concentration occurred, food organisms were not uniformly distributed because some species were concentrated at the surface during the day. In Card Sound and Biscayne Bay the mean annual concentration of food from the 200-μm net (the size range fed to adult *Sagitta* and postlarval *Mnemiopsis* in our experiments) was 0.8 and 8.1 μgC/liter. Taking into account all organisms down to a 20-μm retaining mesh those figures would be increased by a factor of 5 (Reeve and Cosper 1973).

Production Comparisons

Sameoto (1971) obtained a value for the net production of *S. elegans* in Nova Scotia waters (ranging in temperature approximately from 0.5° to 14°C) of 200 mgC/m^2 per yr in a 50-m water column, and McLaren (1969) reported a similar range of values for this species from Ogac Lake on Baffin Island (49-196 and 318). Those authors estimated production/biomass ratios between 1.0 and 2.1 on an annual basis. These figures compare with annual net production of *S. hispida* in Card Sound and estimated in Biscayne Bay of 730 and 1,750 mgC/m^2 per yr and production/biomass ratio of 109 on an annual basis. With a mean annual biomass two orders of magnitude lower, therefore, *S. hispida* in Card Sound exceeds the net production of *S. elegans* in St. Margaret's Bay, Nova Scotia by virtue of its rapid growth rate and short generation time. The disparity would be even greater on a cubic meter basis because Card Sound is comparatively shallow.

Hirota (1974) quoted a value for net annual production of the ctenophore *Pleurobrachia bachei* in waters off California (ranging in temperature approximately from 12.5° to 20°C) of 5,415 mg ash-free dry weight/m^2 per yr, and a daily production/biomass ratio of 0.02. These figures compare with an annual net production of *M. mccradyi* in Biscayne Bay of 2,086 to 4,227 mg ash-free dry weight/m^2 per yr and a production/biomass ratio of 0.12. As in the previous comparison, annual production of different species in different regions is surprisingly similar on a water column (square meter) basis. The growth rate of *M. mccradyi*, however, is some 5 times faster, and its production is supported by a water column depth of 3 m rather than in excess of 40 m in the case of *Pleurobrachia bachei*.

The 10-fold difference in the mean annual standing stock of 200-μm mesh zooplankton between Card Sound and Biscayne Bay (and in phytoplankton pigment) is probably a reflection of the poor water exchange and limited land drainage into Card Sound as compared with Biscayne Bay (Reeve and Cosper 1973). These

differences in plankton biomass are accompanied by differences in biomass for both *Sagitta* and *Mnemiopsis*. In surface net tows from the 200-μm mesh, the biomass of the chaetognath in Biscayne Bay is 2.4 times that in Card Sound. The ctenophore is totally absent from Card Sound (except for rare isolated individuals). Baker (1973), relating stations with low plankton standing stock to low ctenophore levels in Biscayne Bay, suggested that the Card Sound plankton could not support a ctenophore population.

Since the waters of Card Sound are contiguous with those of Biscayne Bay to the north, and neritic waters to the east, where ctenophores are often abundant, the phenomenon of their exclusion from Card Sound can hardly be a physical one. A possibility is that chaetognaths are more efficient in collecting food at lower densities than are ctenophores.

It is of interest that the seasonal variations of biomass and production of the ctenophore populations both in Biscayne Bay and off California are extreme, to the extent that in both cases the months of peak production account for about two-thirds of the annual total. In the case of *S. hispida* this value is about one-fifth. There is probably some correlation between this extreme population instability of *M. mccradyi* and the suggestion above that its absence from Card Sound is related to its inefficiency in collecting food at low concentrations compared to *S. hispida*. The dry weight of other zooplankton from the 200-μm mesh net in Card Sound (Reeve and Cosper 1973) never exceeds the minimum value in central Biscayne Bay (Baker 1973).

It is possible to get a rough estimate of the relationship between production of *S. hispida* and *M. mccradyi* and the rest of the zooplankton by utilizing the standing stock data for that period in the two reports referred to immediately above. The mean annual dry weight of zooplankton (excluding ctenophores and corrected for detritus) was 2.02 and 5.28 mg/m^3 in the 200- and 64-μm mesh net respectively in Card Sound and 19.8 mg/m^3 in the 200-μm mesh net in central Biscayne Bay. Assuming the ratio between 64- and 200-mesh plankton in Card Sound is applicable to Biscayne Bay, and the ash-free dry weight is the same percentage of dry weight as determined for *S. hispida*, the mean annual ash-free dry weight in Card Sound and central Biscayne Bay was 6.62 and 64.9 mg/m^3 respectively. Since it appears that even the youngest larvae of *Mnemiopsis* and *Sagitta* do not utilize food organisms much smaller than those retained by the 64-μm mesh, and since neither carnivore appears to be able to utilize other sources of potential food such as detritus or phytoplankton (Reeve and Walter 1972; Baker and Reeve 1974), the plankton biomass quoted above is the only source of nutrition for these carnivores. If a production/biomass ratio the same as that determined for *S. hispida* is applied to these biomass figures, the net production available to these carnivores is 2.05- and 20.1-mg ash-free dry weight/m^3 per day. Since these figures are for surface waters, they may be related to the equivalent values for *Sagitta* and *Mnemiopsis* derived earlier. The daily net production of *S. hispida* in Card Sound and Biscayne Bay is then 47.7 and 11.7% of the production of potential food in those areas. For *M. mccradyi* in Biscayne Bay it was 9.5 or 19.2% depending on which production peak was included (see above). The total percentage for the two species is then 47.7 for Card Sound and 21.2 or 30.9 for central Biscayne Bay. If the ratio of production to food ingested is taken to be 50% on the basis that immature animals are responsible for most of the production, and would have higher growth efficiencies than the 30-40% range for adults quoted by Reeve (1972), then the chaetognaths in Card Sound appear to utilize all the rest of the zooplankton above 64 μm. For Biscayne Bay, the chaetognaths and ctenophores together utilize between 40 and 60% of the available food. As explained earlier, these are overestimated because the growth rates were maximum growth rates, but they do support the contention that there is little potential food reserve in Card Sound for other carnivores, and that *Sagitta* is more efficient in competing for the available supply. This is in agreement with the fact that in Card Sound, its population was as high as 42% of that in central Biscayne Bay, while for larger decapod larvae, fish larvae, and ctenophores (the other major first-order plankton carnivores) the values were approximately 25, 25 (see Reeve in press), and 0%.

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EFFECTS OF ACCLIMATION ON THE TEMPERATURE AND SALINITY TOLERANCE OF THE YOLK-SAC LARVAE OF *BAIRDIELLA ICISTIA* (PISCES: SCIAENIDAE)[1]

ROBERT C. MAY[2]

ABSTRACT

Eggs of the bairdiella, *Bairdiella icistia*, were fertilized and incubated in various combinations of temperature and salinity, and the salinity and upper thermal tolerances of the yolk-sac larvae were determined. The upper thermal tolerance was enhanced by acclimation to high temperatures and low salinities. Acclimation to low salinities enhanced the lower salinity tolerance of larvae at 24 h after exposure to test conditions, but an acclimation effect on the upper salinity tolerance was not apparent until 48 h after exposure. Yolk-sac bairdiella larvae are more tolerant than the embryonic stages and less tolerant than adults to extremes of temperature and salinity.

Techniques for inducing gonadal maturation and spawning under laboratory conditions are well developed for the bairdiella, *Bairdiella icistia* (Jordan and Gilbert), a sciaenid fish native to the Gulf of California and now present in the Salton Sea (Haydock 1971; May 1975). Hence bairdiella eggs and larvae are extremely favorable material for studying various facets of early development in a marine fish, and detailed information on the effects of temperature and salinity on fertilization, embryonic development, and hatching in this species has already been presented (May 1975). The present paper is concerned with the effects of acclimation on the tolerance of yolk-sac bairdiella larvae to temperature and salinity.

Acclimation has been defined as "the process of bringing the animal to a steady state by setting one or more of the conditions to which it is exposed for an appropriate time before a given test (Fry 1971:14)." In the case of yolk-sac larvae of tropical fish species which develop very rapidly, the term acclimation has a somewhat special meaning, since it necessarily refers to the conditions obtaining during embryonic development. Virtually no studies of acclimation in this context have heretofore been published. Although salinity has been shown to affect the upper thermal tolerance of adult fish (e.g., Garside and Jordan 1968), no comparable work has been reported for fish larvae. This paper investigates the upper thermal tolerance of newly hatched bairdiella larvae and the modifying influence of acclimation, i.e., the influence of temperature and salinity during embryonic development. Since there is little likelihood that bairdiella larvae would encounter lower lethal temperatures in nature (May 1975), their lower thermal tolerance is not considered here. In addition to upper thermal tolerance, the upper and lower salinity tolerance of larval bairdiella and the effect of the acclimation salinity are also considered in this paper. This information, together with results on embryonic tolerances described earlier (May 1975) and available information concerning adult tolerances, should lead to a conclusion as to which stage in the life history of bairdiella is the most sensitive to temperature and salinity.

METHODS

General

Bairdiella eggs were obtained from fish which had been held in normal seawater (33‰) and induced to mature and spawn in the laboratory, as described previously (May 1975). Eggs were artifically fertilized at specified temperatures (within ±0.2°C) and salinities (±0.5‰) and maintained under the same conditions until hatching in specially designed incubators (May

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1975). These conditions (which remained constant from fertilization to hatching, plus the period of time between hatching and transfer to the test conditions) constituted the conditions of acclimation. Larvae were not fed during the experiments. Test salinities were prepared by dilution with deionized water from a stock solution of 60‰, which had been made by adding artificial sea salts to seawater (May 1975).

Upper Thermal Tolerance

Larvae were acclimated to temperatures of 21°, 24°, 27°, and 30°C, and to salinities of from 15 to 45‰ (Table 1), covering the ranges of these two factors within which successful embryonic development can take place (May 1975). Since developmental rates were more rapid at the higher temperatures (May 1975), the period of acclimation (fertilization to transfer to test vials) was shorter at the higher acclimation temperatures. The median tolerance limit (TLm)[3] of yolk-sac larvae to high temperatures was determined by the method of Doudoroff (1942). Larvae were transferred directly from the acclimation conditions to a series of 25-ml capped vials maintained in the dark at a series of high temperatures in a thermal gradient block (Thomas et al. 1963) within 5 to 10 h after hatching, at which time they were 1.8 to 2.0 mm in length. The highest test temperature was 36°C, and between five and eight test temperatures, 1.5°C apart, were used depending on the acclimation temperature; the salinities in the test vials were the same as the acclimation salinities. Approximately 10 larvae were placed in each vial, and the test temperatures did not vary by more than ±0.1°C. Antibiotics were added to the water in the vials (May 1975), and the survival of larvae under optimal conditions in these vials was comparable to that in larger containers. The number of larvae surviving at each test temperature was recorded at 0.5, 1, 3, 6, 12, 24, 48, and 72 h after transfer, and for each time the TLm—the temperature at which just 50% of the larvae survived the given time interval—was estimated by graphical interpolation as described by Doudoroff (1942). At each observation, larvae which showed no movement were removed from the vials by pipette and examined under a dissection microscope. If the heart was not beating and the larva was opaque, the larva was considered dead and was discarded; live larvae were returned to the vials. In one instance (see Results) moribund larvae were found and counted as dead.

Salinity Tolerance

Larvae were acclimated to salinities of 15, 20, 25, 30, 35, and 40‰, and their upper and lower salinity TLm's were determined by transferring larvae directly to a series of 25-ml vials containing test salinities ranging from 0 (deionized water) to 58‰. Between five and seven larvae were transferred to each vial within 8 h after hatching. Because of limited material, only the upper TLm was determined for larvae from an incubation salinity of 40‰, and only four larvae from this salinity were available for each vial. The temperature during fertilization, incubation, and testing was maintained at 24 ± 0.2°C by thermostatically controlled water baths, and vials were kept under continuous room light of low intensity (May 1975). The number of larvae surviving at each salinity was recorded 24, 48, and 72 h after transfer, and the upper and lower TLm's were estimated graphically for each time interval as in the case of thermal tolerance. Larvae were considered dead on the basis of the same criteria used in the study of thermal tolerance.

[3]The term "median tolerance limit" and the symbol TLm are recommended in "Standard Methods" (American Public Health Association 1971).

TABLE 1.—Acclimation conditions for larvae used in determination of heat tolerances.

Acclimation salinity (‰)	Acclimation temperature (°C)			
	21	24	27	30
15	×		×	
20		×		×
25	×		×	
30		×		×
35	×		×	
40		×		
45	×			

RESULTS

Upper Thermal Tolerance

The upper TLm dropped with increasing time intervals (Figures 1-4), and there was a leveling off of the time-temperature curves in the lower salinities as time increased. Most of the time-temperature curves have been separated by eye-fit lines into two major segments, the horizontal segment defining the "incipient lethal temperature"

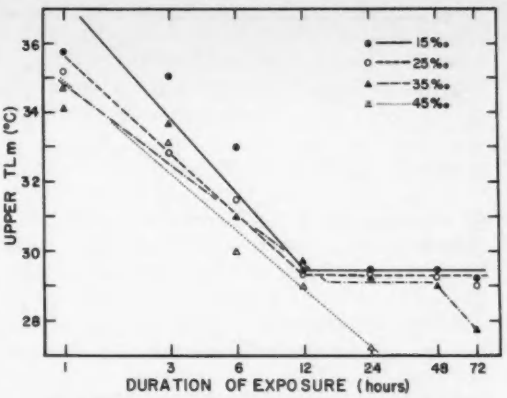

FIGURE 1.–Heat tolerance of larval bairdiella acclimated to 21°C in various salinities. The upper median tolerance limits (TLm) are plotted for various durations of exposure. The time scale is logarithmic, and lines were fitted by eye.

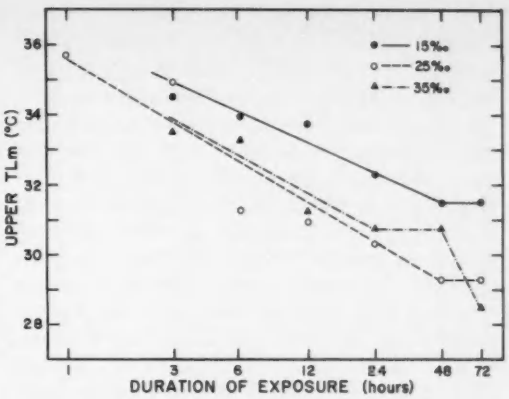

FIGURE 3.–Heat tolerance of larval bairdiella acclimated to 27°C in various salinties.

(Brett 1956), but in several curves there is a suggestion of an early plateau during the first few hours of exposure to the test conditions (Figures 1, 3, 4). At any given time the TLm was usually higher in the lower salinities. Since the highest test temperature used in the experiments was only 36°C, at acclimation temperatures above 21°C the 50% mortality point was usually not reached until 3 or more hours after exposure to the test conditions. Survival was very poor among larvae from eggs maintained at 30°C (a temperature highly stressful to eggs–May 1975) in 30‰, and at 24 h, survival in this group was below 50% at all test temperatures. For purposes of comparison, the 24-h upper TLm has been plotted against salinity for various acclimation temperatures (Figure 5); in this graph the increase in TLm at lower salinities is clear, as is the general increase in TLm effected by higher acclimation temperatures. In a salinity of 15‰, all larvae alive at 12 and 24 h in the 21°C acclimation group were moribund in test temperatures of 30°C and higher, i.e., they were contorted and totally immobile and unresponsive to touch, although their hearts were beating and they were not opaque. These larvae have been considered dead for the purpose of data presentation; if considered alive, they would raise the calculated 12-h upper TLm from 29.5° to 32.1°C (Figures 1, 5). At the salinity of normal seawater, the 24-h upper TLm of larval bairdiella lies

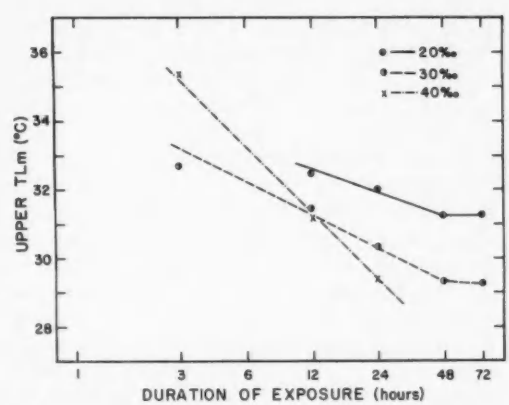

FIGURE 2.–Heat tolerance of larval bairdiella acclimated to 24°C in various salinities.

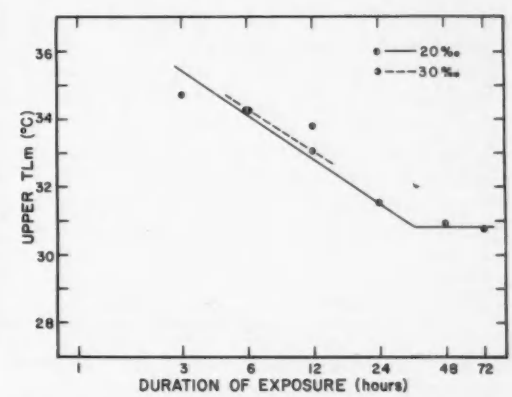

FIGURE 4.–Heat tolerance of larval bairdiella acclimated to 30°C in two salinities.

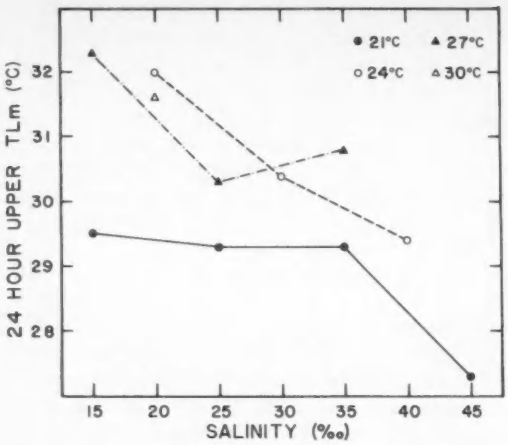

FIGURE 5.—Twenty-four hour upper median thermal tolerance limits (TLm) at various salinities for larvae acclimated to 21°, 24°, 27°, and 30°C.

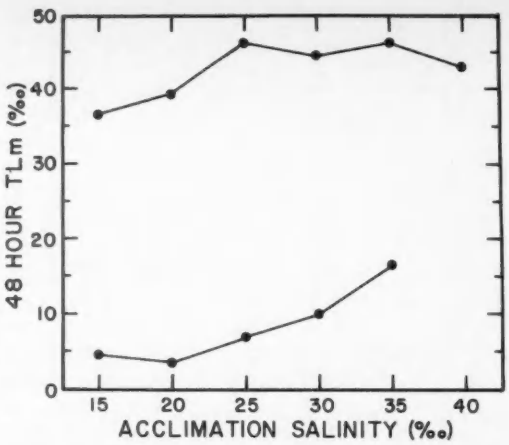

FIGURE 7.—Upper and lower median tolerance limits (TLm) of salinity for a 48-h exposure.

between 29° and 31°C, depending on the acclimation temperature. Larvae could resist higher temperatures for shorter periods of time.

Salinity Tolerance

The 24 h upper TLm for salinity was not greatly affected by the acclimation salinity and ranged from 43 to 48.5°/₀₀, but the 24-h lower TLm was appreciably higher among larvae incubated at higher salinities (Figure 6). The lower TLm's (24 h) for larvae acclimated to 15 and 20°/₀₀ were 4.2 and 3.5°/₀₀, respectively, whereas those for larvae acclimated to 30 and 35°/₀₀ were 10 and 16.5°/₀₀, respectively. The major difference between the 24-h TLm's and those for 48 and 72 h is the progressive lowering of the upper TLm for larvae acclimated to low salinities (Figures 7, 8). The upper TLm for larvae from 15°/₀₀ shifted from 46.2°/₀₀ at 24 h, to 36.6°/₀₀ at 48 h, and to 30.0°/₀₀ at 72 h; between 24 and 72 h, the upper TLm remained the same (43°/₀₀) for larvae acclimated to 40°/₀₀, and decreased only from 48 to 46.2°/₀₀ for

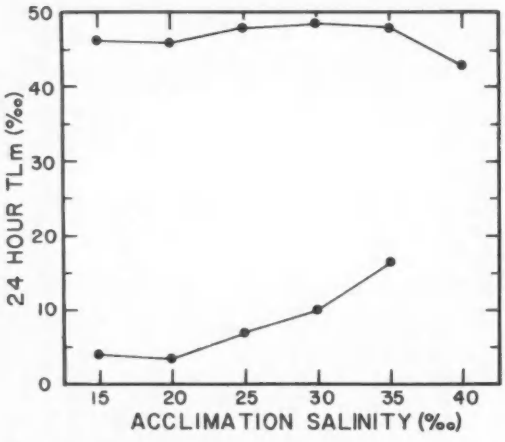

FIGURE 6.—Upper and lower median tolerance limits (TLm) of salinity for a 24-h exposure. Larvae were acclimated to various salinities at 24°C.

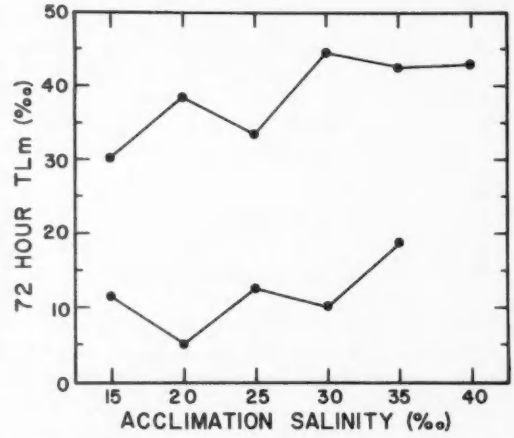

FIGURE 8.—Upper and lower median tolerance limits (TLm) of salinity for a 72-h exposure.

those acclimated to 35°/∞. There was little change in the lower TLm's between 24 and 48 h, but a slight rise occurred between 48 and 72 h in all but the 30°/∞ acclimation group.

DISCUSSION

Fry et al. (1946) define the "zone of tolerance" as the range of any environmental factor within which an animal can live indefinitely, and the "zone of resistance" as the range within which the animal can live for only a finite period of time, depending on the level of the factor. The zone of tolerance is bounded by the upper and lower "incipient lethal levels." In work on the upper thermal tolerance of fishes, the incipient lethal level is defined by an abrupt flattening of the time-temperature curve at a temperature below which less than 50% of the exposed individuals succumb (Brett 1956). Some of the curves generated in the present study (Figures 1-4) suggest that the incipient lethal level has been reached, but curves from the higher salinities lack a horizontal segment. This points up a difficulty in working with early larvae: at 24°C the larval yolk supply is 95% consumed by about 40 h after hatching (May 1974), and this occurs even sooner at higher temperatures. The 48- and 72-h TLm's therefore apply to starving larvae. Unlike adult fish, larvae which hatch from pelagic eggs are extremely sensitive to food deprivation (e.g., Lasker et al. 1970) and begin dying of starvation soon after yolk absorption if food is not provided for them, and unfed bairdiella larvae die sooner at high temperatures and salinities (May 1975). Therefore, prolonging these tests would not have helped in defining the upper incipient lethal temperature for larvae in the higher salinities—the TLm would simply continue to fall. Even at the lower salinities, the TLm would decline after a sufficient period of time; the curves for a salinity of 35°/∞ (Figures 1, 3) show how a flat segment is reached, only to be followed by another drop in TLm. A further difficulty in estimating tolerance limits for warmwater larvae is that these larvae develop morphologically at an extremely rapid rate and are very different organisms 1 or 2 days after hatching than they are at hatching. Newly hatched bairdiella are poorly developed and rather inactive (May 1975), whereas by 45 h after hatching (at 24°C) they have acquired functional eyes and an open mouth and are quite active. In this situation, consideration of the TLm at a more or less arbitrary time after exposure to the test conditions, such as 24 h, is at least a useful approach for comparative purposes.

Larval bairdiella are more sensitive to high temperatures when the salinity is also high, as are bairdiella gametes and developing embryos (May 1975). This adds further weight to the suggestion (May 1975) that in nature, eggs spawned late in the season at high temperatures will have a reduced chance of contributing recruits to the population when natural salinities rise as they are doing in the Salton Sea. The survival of bairdiella larvae in the Salton Sea would be significantly reduced at temperatures above 31°C, and temperature data from the Salton Sea (May 1975) indicate that some larvae could be exposed to thermal stress of this level or greater. The highest TLm is reached in 15°/∞, the lowest salinity in which larvae were tested and the nearest to being isosmotic with larval body fluids. Older fishes of various species are also most tolerant of high temperatures in isosmotic or nearly isosmotic salinities (Arai et al. 1963; Strawn and Dunn 1967; Garside and Jordan 1968; Simmons 1971). The added burden of osmotic work seems to reduce the ability of both larval and adult fish to tolerate extremely high temperatures.

It is clear that acclimation can alter the tolerance of early bairdiella larvae to both temperature and salinity, even though the rapid developmental rate of bairdiella eggs restricts the period of acclimation to between 20 and 40 h (the time between fertilization and transfer to test conditions, which is a function of incubation temperature). Incubation of bairdiella eggs at higher temperatures produces larvae with a higher upper thermal TLm. However, increasing the acclimation temperature from 27° to 30°C does not increase the upper TLm, even though the TLm's are generally above 30°C. Hence the lethal levels determined for an acclimation temperature of 27°C may represent "ultimate" incipient lethal temperatures (Fry et al. 1946), but here again one must consider the unique problems of working with early larvae. If the effect of thermal acclimation on the tolerance of yolk-sac larvae is to be studied, acclimation must take place during embryonic development, but the embryos are more sensitive to temperature than are the larvae to which they give rise (cf. May 1975). A temperature of 30°C is extremely stressful for developing eggs, and the larvae produced at this temperature survive poorly, a trait magnified at higher salinities.

The response of these larvae to elevated temperatures is therefore not a true reflection of thermal "acclimation," as the term is generally used, but is more a reflection of thermal stress during sensitive periods of morphogenesis. In an analogous way, salinity stress on embryos during acclimation at 40‰ probably accounts for the observation that the larvae have a reduced upper TLm for salinity when compared with larvae acclimated to 30 and 35‰.

Thermal acclimation has also been shown to affect the thermal tolerance of larval herring (Blaxter 1960), menhaden (Lewis 1965), and salmonids (Bishai 1960; Iwai 1962), although only Blaxter's study utilized larvae which hatched from eggs maintained at the acclimation temperature. The mechanisms involved in thermal acclimation during early development have never been investigated, but the present results for bairdiella suggest that they must be activated quite rapidly, within a day or two at most. A similarly rapid rate of acclimation to warm temperatures has been found in older fish (Brett 1970; Allen and Strawn 1971), so that a similar mechanism may be operating in both cases. Factors involved in setting thermal tolerance limits in fishes are little understood (Fry 1967), but thermal inactivation of enzymes has been suggested as a possible mechanism (Hochachka and Somero 1971).

Holliday and Blaxter (1960) found that the salinity prior to hatching had a limited effect on the salinity tolerance of larval herring. This effect was more pronounced in the present experiments with larval bairdiella, but there was a delay in the appearance of the acclimation response to high salinities. The upper TLm (salinity) was similar for all acclimation salinities 24 h after initial exposure to the test conditions, but at 48 h the larvae acclimated to high salinities had a higher TLm than those from low salinities (a very slight indication of the same phenomenon can be discerned in the results of Holliday and Blaxter 1960). This observation is difficult to explain, especially in view of the rudimentary state of our knowledge of larval osmoregulatory mechanisms; perhaps it is related to the opening of the mouth between 35 and 45 h after hatching (May 1974), which could expose the internal larval tissues more directly to the ambient salinity. Incubation at low salinities enables larvae to tolerate much lower salinities than larvae incubated in more saline water. Again, it is difficult to speculate on how this effect might be mediated.

Early larvae of *Bairdiella icistia* are more tolerant than the embryonic stages and less tolerant than adults to extremes of temperature and salinity. Very few bairdiella eggs develop normally at 30°C (May 1975), and 15 to 40‰ is the approximate salinity range for normal fertilization and embryonic development. In contrast to the eggs, 50% of the newly hatched larvae are capable of withstanding temperatures between 30° and 33°C for 24 h or longer, except at the lowest acclimation temperature and highest salinity; and with proper acclimation, larvae can tolerate salinities ranging from about 4 to 48‰ for 24 h, or 5 to 45‰ for 72 h. Juvenile and adult bairdiella must tolerate temperatures ranging from 10° to 34° or 35°C in the Salton Sea (Carpelan 1961). These fish have been found in freshwater (R. G. Hulquist, California Department of Fish and Game, pers. commun.) and can tolerate Salton Sea water with a salinity of 52.5‰ for 96 h after direct transfer from ordinary Salton Sea water (approximately 38‰), and 58‰ for over a week after gradual acclimation (Hanson 1970). The early larvae of some other species have also been shown to be more tolerant of temperature and salinity than their eggs. McCauley (1963) reports that prolarvae of the sea lamprey, *Petromyzon marinus*, are considerably more tolerant of high temperatures than are the eggs, and data presented by Holliday (1965) show that newly hatched herring, *Clupea harengus*; plaice, *Pleuronectes platessa*; and Atlantic cod, *Gadus morhua*, larvae are more tolerant of both high and low salinities than are their respective eggs. However, in the case of the herring and plaice, further larval development and metamorphosis are accompanied by a decrease in salinity tolerance (Holliday 1965), a pattern quite different from that found in bairdiella.

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THE INTERACTION OF ECONOMIC, BIOLOGICAL, AND LEGAL FORCES IN THE MIDDLE ATLANTIC OYSTER INDUSTRY

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ABSTRACT

Economic, environmental, and legal forces are contributing factors in the decline of the Middle Atlantic oyster industry. This paper determines the interactions and importance of these forces by quantifying and integrating some of the relevant variables into a supply and demand model of the oyster industry. The statistical results yield significant and expected parameter values with useful information on price and income demand elasticities. Also implications of common property legal frameworks on resource utilization are revealed. The main conclusions are that efforts to rehabilitate the industry by cleaning up pollution, replacing cultch, and encouraging legal private property rights may have large social values.

The historically important Middle Atlantic oyster industry is currently recognized as having many of the symptoms of a declining industry. Economic, biological, and legal forces are contributing causal factors in the fishery's decline. This paper attempts to integrate some of these variables into an estimable supply and demand model explaining oyster price and output movements over time for the region. Economic and biological variables are directly included in the model while the legal dimension is focused on indirectly by comparing empirical results for data generated from different common property structures.

The multidimensional approach reveals information on price and income elasticities, substitutability relationships, and the effect a common property regulatory framework has on resource overutilization and depletion. The regional orientation taken in this paper, rather than a national or international focus, provides a departure from much of the traditional fishery analysis and enables the effects of alternative property right structures between states to be observed.[2]

The impact property rights structure has on economic efficiency and biological growth has been discussed widely in the theoretical literature of fishery modelling.[3] Less however has been written on empirical analyses of the effects property rights have on economic and biological efficiency.[4] Consensus among the discussants is that common property leads to overexploitation of fish stocks and perhaps extinction of a species. Common property right systems result in less efficient resource allocation than private right systems since the former do not ensure that the total costs of an individual harvester's exploitation of the resource are borne fully by him. Private property internalizes the costs of the harvester's actions thereby forcing the producer to bear not only all of the costs of his actions but also to capture all of the benefits.

MIDDLE ATLANTIC OYSTER FISHERY

The American Eastern oyster represents the resource base of both the Gulf and Atlantic coasts oyster industries. Following a brief mobile larval stage, the oyster connects permanently to a firm subaqueous material such as rock or shell deposits.

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[2]Recent empirical work confined primarily to economic factors and directed towards species and regions different from our analysis includes Bell (1968), Doll (1972), and Waugh and Norton (1969).

[3]Much has been written in fishery economics on the effects of biological stock depletion due to common property legal structures. Some of the earlier treatments that are still widely referred to can be found in Gordon (1954) and Scott (1955). For more recent theoretical analyses see Fullenbaum et al. (1972), and Smith (1969). In the context of this literature, common property means that any member of a community has the right to harvest the fish stock.

[4]Notable exceptions in the fishery literature where the effects of legal ownership frameworks have been quantified include Bell (1972) and O'Rourke (1971). For example Bell estimates the redundant effort employed in the American lobster fishery which is subject to common property. He concludes that approximately 50% of current fishing effort is required to achieve economic efficiency.

Also the authors, in an unpublished paper (Efficiency and Property Rights in the U.S. Oyster Industry, 1974), estimate that in 1969 oystermens' income would have increased by almost 50% if all coastal states had relied on leasing of oyster beds.

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Its habitat is the intermediate salinity waters of the seacoast's intertidal zone and of inland rivers and bays. Water current, temperature, and biological productivity, in addition to salinity, are determinants of the resource productivity of a given parcel of subaqueous land.

The property right structure characterizing oyster grounds varies widely among states. Courts have granted rights to subaqueous land to the people of each state for their own common use. State legislatures exercise these rights. The federal government has been granted the right to a 3-mile coastal zone and Congress in turn has ceded back to the states land and resource use rights within this zone.[5] States have responded in similar ways to the exercise of their rights to the oyster resource. In general, natural oyster beds have been set aside as a common fishery for state residents,[6] whereas other submerged land parcels are available for private leasing. However, great variation among the states exists in the proportion of area and quality of land set aside for public or common use versus private use depending on how broadly administrators define the term "natural oyster bed."[7] An examination of the proportion of oyster catch by weight on private grounds to total catch by state reveals ratios ranging from a maximum of 1 to 0 for certain states in recent years. Within the Middle Atlantic region the two states with property rights in Delaware Bay (i.e., Delaware and New Jersey) can be characterized as essentially private property states, whereas Maryland and Virginia, which share the Chesapeake Bay, have significantly lower private to total catch ratios.[8]

Private property rights in oystering tend to promote efficiency in several ways. First, exclusive user rights provide incentives for firms to pursue a policy of investing in cultch and maintaining it at a desired level as influenced by market conditions. Second, congestion and overexploitation of the oyster resource is unlikely to occur since there is no pressing need to harvest quickly so as to not lose the resource's benefits. Finally, a communal property structure tends to lower efficiency by requiring the use of obsolete technology in order to prevent depletion of the resource stock. Inefficient technology often takes the form of obsolete capital regulated into use by legislative codes. In general, states relying on common property right structures tend to impose greater restrictions on the use of capital than private property states.[9]

Between 1947 and 1968 the annual U.S. domestic oyster harvest declined from 63.1 to 55.6 million pounds. Imports increased from an insignificant 111 thousand pounds to 15.5 million pounds during the same years. Accounting for inventory changes, total consumption of oyster meat consequently expanded by 8.2 million pounds. Concurrently, both ex-vessel and wholesale prices rose. Between 1950 and 1968 ex-vessel prices rose 38% and wholesale prices rose 89%.[10]

Significant regional differences in oyster catch trends characterize the post-World War II period. In general, the Gulf region has increased its landings while landings in the Middle Atlantic region (defined to include the states of New York, New Jersey, Delaware, Maryland, and Virginia) have declined by 45%. Delaware and New Jersey harvests especially have fallen dramatically, no doubt in large part due to disease which affected stocks beginning in 1958. It is during this period of both relative and absolute decline that we shall estimate the underlying factors explaining changes in quantities and prices for the Middle Atlantic oyster industry.

MODEL

Economic variables such as prices and quantities are generally explained by economists through the use of supply and demand models. Prices and quantities are determined through the equilibration of supply and demand forces which incorporate the effects of various predetermined

[5]See Power (1970) for a detailed description of court decisions involving rights to submerged land.

[6]Legislative codes usually prohibit nonresidents from entering the industry. See Power (1970:216-223) for a discussion of the constitutionality of these restrictions.

[7]Maryland, for example, classifies a natural bed as one such that the natural growth of oysters "... is of such abundance that during the preceding five years the public has resorted to them for livelihood," Power (1970:220). Courts reportedly view one individual declaration of one day's work in a 5 yr period as sufficient evidence of the existence of a natural bed. Most states employ a less restrictive definition for a natural bed.

[8]It is useful to note that private property rights may be institutionally arranged in a multitude of ways. The usual manner of leasing subaqueous lands to a relatively few individuals is by no means the only way of introducing private property, and in fact is often objected to as prejudicial to individual freedom. A more acceptable arrangement pointed out by a reviewer may be for states to assume control of beds and issue permits to harvest a given quantity of oysters.

[9]For example, in the predominantely common property right state of Maryland power dredging is prohibited in the harvest of oysters. Consequently any dredging takes place through the use of sail-powered craft called skipjacks, the newest of which is around 50 yr old.

[10]All data presented in this section are from *Fishery Statistics of the United States*, Bureau of Commercial Fisheries. National retail price data are not readily available.

(independent) variables on the endogenous (dependent) variables price and quantity. A general application of this methodology to any commodity would specify that quantity supplied (Q_s) is dependent on input cost factors, prices of goods related in supply, and price of the product. Quantity demand (Q_d) is usually hypothesized to depend on current price, income, and prices of related goods in demand.

When specifying such a model for oyster markets several modifications to the supply specification of the above general framework are employed. Although from supply theory input factors include technological, environmental, and biological variables, data limitations restrict the inclusion to a single biological factor, the MSX disease.[11] It is hypothesized that the protozoan oyster parasite commonly referred to as the MSX disease has a negative impact on the oyster industry during the period of analysis. Also since no strong relationships between the production of oysters and other goods is readily apparent, we omit prices of related goods from the oyster supply relationship.

The last modification of the supply relationship for oysters and probably the most unique feature of the model is the hypothesis that quantity supplied is a function of price lagged 1 yr rather than current price. As in the case of agricultural commodities, quantity supplied of oysters can be considered a function of past price and natural phenomena and hence fixed in the short run. In the fishery case a fixed supply is usually based on the presence of lags in generating fishing effort (e.g. securing capital and making occupational choices). Lagged price can be expected to positively influence current fishing effort.[12] In fishery estimation with annual data however, the assumption of such long lags in adjusting fishing effort may be inappropriate and the inclusion of lagged price as a determinant of effort will likely be a weak determinant of supply.

An additional rationale is therefore necessary for including price lagged 1 yr as a determinant of supply. We hypothesize that lagged price has a negative impact on current supply due to a depletion effect. In fishery production not only current effort, but current biological stock determines current production. If current biological stock is negatively related to past effort, then variables explaining past effort may bear a strong relation to current supply. Price lagged 1 yr (or alternatively distributed lags of past prices if data were plentiful) may be closely related to past effort. Accordingly we hypothesize that price lagged 1 yr is a proxy for past levels of effort and thus negatively related to current biological stock. Also if the negative relationship that lagged price has on current biological stock is strong enough to offset the positive relationship lagged price has on current fishing effort, the net impact of lagged price on current supply might be negative.

Furthermore we expect the negative depletion effect of lagged price to be stronger in fisheries subject to common property. Thus lagged price is likely to have a slight positive effect on supply in fisheries subject to private property due to the positive effort effect. For fisheries subject to common property the negative depletion effect is expected to offset the positive effort effect yielding a negative relationship between lagged price and quantity supplied.

The structural equations and equilibrium condition of the fixed supply model applied to oyster markets are written below with expected parameter signs appearing above each explanatory variable.

$$\text{Supply } Q_s = S(\overset{-}{\text{MSX}}, \overset{+}{P_{t-1}})$$

$$\text{Demand } Q_d = D_1(\overset{-}{P}, \overset{+}{I}, \overset{+}{P_r})$$

$$\text{Equilibrium conditions } Q_s = Q_d = Q$$

where MSX, P_{t-1}, P, I, and P_r are the MSX disease, price lagged 1 yr, current price, income, and the price of a related good, respectively. In the supply equation a negative relationship with MSX is hypothesized a priori, and lagged price may be positive or negative depending on the intensity of depletion. In demand, current price is expected to have a negative effect according to the law of

[11]Little technological change has occurred during the period of analysis due in part to state regulation mandating old technologies as a conservation device. Environmental factors such as pollution and siltation have doubtless had a negative impact on oyster supplies, but unfortunately little systematic and consistent information is available through time.

[12]We note that although lagged price may positively affect current effort the total effect on current harvest (i.e. supply) depends on what effect lagged price has on the current biological stock of the resource. For reasons explained below the net affect of lagged price on current supply might actually be negative if stocks have been reduced to the point of depletion. For an example of the short-run supply assumption (i.e., supply is independent of current price) in the fishery area, see Bell (1968). It should be noted that Bell's empirical work is quite successful using monthly data.

demand, the income effect is positive if oysters are a normal good, and the related good (poultry) is most likely a substitute for oysters.

Since the fixed supply assumption removes the simultaneity from the model, both the supply and demand functions can be interpreted as reduced forms, and estimated directly by ordinary least squares regression techniques without regard to problems of identification. The demand function is solved for its only endogenous variable, price, and estimated in this form. The reduced form equations estimated later in the paper are written below.

$$\text{Supply } Q = S(\overset{-}{\text{MSX}}, \overset{+}{P_{t-1}})$$

$$\text{Demand } P = D_2(\overset{+}{I}, \overset{+}{P_r}, \overset{-}{Q})$$

where Q is predetermined.

In addition to conclusions concerning parameter signs and elasticity values, implications of property right structures are revealed in the model. It is hypothesized that in states relying more heavily on common property rather than private leasing of subaqueous beds, the depletion effect should be greater. The lagged price variable in supply should thus have a negative coefficient value for common property right areas.

DATA

Regression analyses are performed on the above model for the Middle Atlantic and Delaware Bay regions. The Middle Atlantic region is defined to include the five contiguous coastal states of Virginia, Maryland, Delaware, New Jersey, and New York. This region includes the productive subaqueous resources of Chesapeake Bay, Delaware Bay, and part of Long Island Sound. The Delaware Bay area includes the states of Delaware and New Jersey only. We anticipate depletion to be a more important factor in the regional analyses which are dominated by the high production levels of Maryland and Virginia. These Chesapeake Bay states (especially Maryland) rely to a greater extent on common property than do the Delaware Bay states. The latter states allow much more extensive private leasing, and hence supply a greater proportion of their oysters from private leaseholds which may be expected a priori to be less subject to overfishing with the ensuing depletion.

Time series annual data on quantities landed (in pounds) and implicit prices are obtained from *Fishery Statistics of the United States* (1940-1970) compiled by the Bureau of Commercial Fisheries of the U.S. Department of Commerce and the U.S. Department of the Interior. Data on the price of a related commodity in demand (i.e., the price of poultry) and personal income are obtained from the Bureau of Labor Statistics (U.S. Department of Labor) and the *Survey of Current Business* (U.S. Department of Commerce), respectively. The biological variable representing the MSX disease included in the oyster supply function of the model was obtained from site sampling of oysters in the Delaware River.[13] The regions of consumption and production are not identical in that the consumption area includes a somewhat larger area. Precise definitions of the variables used are given below.

- Q Quantity per capita of oyster landings (measured as pounds per person) for Delaware Bay includes Delaware and New Jersey, and regional quantities include the five states of Delaware, New Jersey, Maryland, Virginia, and New York. Population refers to the seven-state region including New York, Pennsylvania, New Jersey, Delaware, Maryland, District of Columbia, and Virginia.
- P Price of oysters measured in dollars per pound (meat weight).
- P_{t-1} Price of oysters lagged 1 yr.
- MSX Biological variable referring to a protozoan oyster parasite commonly called the MSX disease.
- I Personal income per capita (deflated by the Consumer Price Index for all items) for the seven-state region including New York, Pennsylvania, New Jersey, Delaware, Maryland, District of Columbia, and Virginia.
- P_{ch} National average price per pound for chickens (live weight).

EMPIRICAL RESULTS

We now turn to a brief discussion of the detailed findings, and conclude with some general remarks and policy implications. Tables 1 and 2 present the

[13]The average annual prevalence of the MSX disease in a test sample of oysters in the Delaware River was obtained from H. Haskin of Rutgers University. These percentages were zero before 1957 and exceeded 50% in some later years.

TABLE 1.—Middle Atlantic supply and demand regressions.

Equation	Endogenous variable	Constant	Predetermined variables					Statistics[1] R^2 DW	Elasticities[2] Price	Income
			MSX	I[3]	P_{ch}	P_{t-1}	Q[3]			
Supply	Q[3]	1.733	−0.581			−1.202		0.85		
			(−3.14)*			−(6.29)*		0.48		
Supply	ln Q[4]	−0.136	−1.001			−0.319		0.68		
			(−3.60)*			−(3.05)*		0.39		
Demand	P	0.802		0.00002	0.010		−0.507	0.54	1.0	
				(0.20)	(4.12)*		(−3.14)*	0.76	0.1	
Demand	ln P[4]	−14.110		1.582	0.425		−0.421	0.53	2.4	
				(3.28)*	(2.59)*		(−1.50)	0.64	3.8	

[1] R^2 and DW refer to the unadjusted coefficient of determination and the Durbin-Watson statistic for autocorrelation, respectively.

[2] The formulae used in calculating price and income elasticities are $\frac{-dQ}{dp} \cdot \frac{P}{Q}$ and $\frac{dQ}{dI} \cdot \frac{I}{Q}$, respectively. In the regressions not utilizing logarithms mean values of variables are used to fix the point elasticities.

[3] Quantity and income are measured in per capita form.

[4] All variables are measured in natural logarithms except MSX.

* Refers to statistical significance at the 0.05 level.

TABLE 2.—Delaware Bay supply and demand regressions.

Equation	Endogenous variable	Constant	Predetermined variables					Statistics[1] R^2 DW	Elasticities[2] Price	Income
			MSX	I[3]	P_{ch}	P_{t-1}	Q[3]			
Supply	Q[3]	0.223	−0.409			0.003		0.70		
			(−8.05)*			(0.22)		0.77		
Supply	ln Q[4]	−1.718	−4.317			−0.155		0.66		
			(−5.99)*			(−0.77)		0.98		
Demand	P	0.165		0.0003	0.008		−1.169	0.55	3.4	
				(3.18)*	(2.43)*		(−2.42)*	1.06	4.1	
Demand	ln P[4]	−18.290		2.090	0.407		−0.170	0.66	5.9	
				(5.04)*	(2.51)*		(−2.51)*	1.24	12.3	

[1] R^2 and DW refer to the unadjusted coefficient of determination and the Durbin-Watson statistic for autocorrelation, respectively.

[2] The formulae used in calculating price and income elasticities are $\frac{-dQ}{dp} \cdot \frac{P}{Q}$ and $\frac{dQ}{dI} \cdot \frac{I}{Q}$, respectively. In the regressions not utilizing logarithms mean values of variables are used to fix the point elasticities.

[3] Quantity and income are measured in per capita form.

[4] All variables are measured in natural logarithms except MSX.

* Refers to statistical significance at the 0.05 level.

empirical results of the supply and demand model applied to oyster data for the years 1940 to 1970 in the Middle Atlantic and Delaware Bay regions. Numerical estimates of the coefficients along with t values in parentheses are obtained through the use of either linear or log linear regression analysis and ordinary least squares as the method of estimation.

In general, parameters have expected signs and are significant for at least the 0.05 level. The coefficient of determination is reasonably high in most regressions indicating that the included predetermined variables explain a large fraction of the variation in the endogenous variables. Since the linear and logarithmic equation forms do not differ greatly there is no evidence of nonlinearities.

In the supply equations the MSX variable displays a strong negative impact on quantity, and is more significant (i.e., larger t values) in the Delaware Bay regressions. Biological evidence indicates that the disease had a greater impact on Delaware Bay production than on Chesapeake Bay production although Virginia was hard hit during much of the period of analysis.

Lagged price has a negative and highly significant impact on supply for the Middle Atlantic region indicating that the depletion effect dominates the effort effect where common property prevails. In contrast the Delaware Bay results indicate that lagged price is not a significant determinant of supply in a private property right structure.

In the price (implicit demand) equations oysters display a significant positive income response in most regressions.[14] Oysters thus appear to be a normal good whose demand is likely to grow as consumer income rises over time. Since the price of chickens is a positive determinant of demand in all regressions, the relationship between the two commodities is one of substitution. The negative coefficient for quantity supports the law of

[14] Preliminary cross sectional analyses conducted by National Marine Fisheries Service Economic Research Laboratory indicate much weaker income effects (and possibly negative) for oysters.

demand indicating demand for oysters to be price-responsive.

In order to determine meaningfully how responsive quantity demanded is to price and income changes, it is useful to investigate the elasticities implied by the statistical results. Tables 1 and 2 indicate high elasticities in both the Middle Atlantic and Delaware Bay regions implying that oysters are price elastic and normal with respect to consumer income responses. If supplies were to increase in the future, one would expect increasing revenues for the oyster industry.[15] Similarly we might expect consumer demand for oysters to increase by larger percentages than real personal income in the future. Efforts to rehabilitate the oyster industry by cleaning up water pollution, discouraging overfishing, and replacing oyster cultch may thus have large social values.

Although the statistical results do lend support to the model, they are certainly not without difficulties. The time series problem of positive serial correlation is present throughout, thus detracting from the reliability of the results. The Durbin-Watson statistics in general indicate either positive autocorrelation or indeterminancy for the Middle Atlantic and Delaware Bay regions respectively using a two-tailed test at the 0.05 level of significance.[16] An additional problem impairing both estimation and prediction is structural change with data over a long time period. Parameters therefore may not remain constant with time series data. Also variables omitted from the model may have caused shifts in the functions over time. All of these problems make prediction hazardous and definitive conclusions should await further testing based on new data sets.

CONCLUSIONS

In general the statistical results support the model of supply and demand forces in the Middle Atlantic oyster industry. Estimates are generated on income and price elasticities of demand and lend optimism to the current rehabilitation efforts directed toward the oyster industry. The MSX disease has clearly had a debilitating effect, however, and must be solved as a condition of successful industry recovery.

The common property characteristics of the industry have also harmed the industry's progress. There exists evidence of overfishing in common property states, and hence less than optimal exploitation of the natural resource stocks. The results indicate that depletion is a much more serious problem for the Chesapeake Bay states than for the Delaware Bay states where private leasing of subaqueous lands is more prevalent. However, the reverse is true concerning the MSX disease characteristics of the regions.

[15] It has been reported by the Delaware State Department of Natural Resources and Environmental Control that oyster spat count recently have been the highest in several years indicating augmented supplies to be highly probable in the future.

[16] When first differences are used to remove serial correlation, R^2 and t values fall to unacceptably low levels although serial correlation is removed.

ACKNOWLEDGMENTS

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THE REPRODUCTIVE BIOLOGY OF THE PROTOGYNOUS HERMAPHRODITE *PIMELOMETOPON PULCHRUM* (PISCES: LABRIDAE)

ROBERT R. WARNER[1]

ABSTRACT

Pimelometopon pulchrum, California sheephead, a labrid fish of the eastern Pacific Ocean, was collected the year round at Catalina Island, Calif., and comparative material was taken at Guadalupe Island, Mexico. Individuals at Guadalupe were dwarfed relative to those at Catalina. *Pimelometopon pulchrum* is a protogynous hermaphrodite, the ovarian elements undergoing massive degeneration as spermatogenic crypts proliferate in the gonads of transitional individuals. Sexual changes occur between breeding seasons. Individuals from both populations mature as females at age four; most of those at Catalina function as females for 4 yr and then change sex, at a length of around 310 mm. Sexual transformation occurs earlier on the average at Guadalupe; most individuals are male by age seven. In both populations, more rapidly growing fishes apparently change sex sooner than other individuals of the same age, and fishes that grow slowly may not change sex at all. Spawning appears to occur in July, August, and September in the Catalina population. Individuals probably spawn several times in a breeding season. The weight of active, prespawning ovaries increases at a rate approximately proportional to the third power of the length of the fish. Ovary weight increases in a linear fashion with age in the Catalina population. The rate of increase with age would be less in the Guadalupe population due to dwarfing.

The three coloration phases of *P. pulchrum* are described, two of which are found in adult individuals. The uniform coloration is made up mostly of mature female and immature fishes. About 5% of the mature uniform individuals were males at Catalina, and about 12% at Guadalupe. The bicolored phase is made up exclusively of males and late transitional individuals. Data from field transects revealed that there were about five uniform individuals to every bicolored male. Based on an estimated yearly survival rate of about 0.7, the mature sex ratio at Catalina was approximately two females for every male. The ratio at Guadalupe was closer to three females for every two males, due in part to the earlier sex changes seen there.

Sequential hermaphroditism, a phenomenon characterized by an individual changing from one sex to another at some point in its life history, is widespread in teleost fishes (Atz 1964; Reinboth 1970). In some species, individuals change from male to female (protandry) and in others the situation is the reverse (protogyny).

Most of the published information on the life histories of sequentially hermaphroditic species has dealt with the distribution of the sexes with size, sometimes correlated with a histological investigation of the gonads (Atz 1964; Reinboth 1970). However, in order to interpret the full implications of the sexual patterns seen in sequential hermaphrodites, data on the age distribution, age-specific fecundity, and the sexual transformation schedule of the population are needed (Warner in press).

There are a few protogynous fish species for which the information is nearly complete. For example, Moe (1969) provided excellent data on the life history pattern, gonadal transformation, and survival rate of the serranid *Epinephelus morio*. Natural sex reversal in the synbranchid *Monopterus albus* has been extensively studied both in the field and laboratory (Liem 1963, 1968; Chan 1971), but little is known about its age-specific fecundity and survival pattern. A similar situation exists for the labrid *Coris julis* (Reinboth 1957, 1962; Roede 1966), where again we lack information on the demography of the population. Among the Labridae, perhaps the most complete information exists on the seven Caribbean species of the genera *Thalassoma*, *Halichoeres*, and *Hemipteronotus* studied by Roede (1972). An unfortunate limitation was placed on Roede's work by the tropical location, which precluded age determination from growth rings on scales or otoliths.

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Pimelometopon pulchrum (Ayres), the California sheephead, is a labrid of the subfamily Bodianinae. It is confined to temperate waters, ranging from Monterey Bay, Calif., to Cabo San Lucas at the tip of Baja California, Mexico (Miller and Lea 1972). Individuals can reach a large size (over 800 mm standard length [SL]) and are commonly found off southern California along rocky shores at depths between 5 and 50 m. In this report, it is demonstrated that *P. pulchrum*, like many other labrids, is a protogynous hermaphrodite. In addition, data are presented on age and growth, on the distribution of the sexes in relation to color, size, and age, and on the observed patterns of fecundity and survival. The study embraces two widely separated populations, chosen to reflect how differences in the demography of the population might lead to the observed differences in the schedule of sexual transformation (discussed in Warner in press).

MATERIALS AND METHODS

Source of Materials and Times of Sampling

Pimelometopon pulchrum was taken by means of a hand spear while either skin diving or using scuba. The main collecting area was at Fisherman's Cove on the northeast shore of Santa Catalina Island, Calif., near the University of Southern California Marine Station (lat. 33°27′N, long. 118°29′W). A total of 341 individuals of *P. pulchrum* were processed from samples taken the year round at monthly intervals. Collections began in December 1969 and continued, with occasional gaps, until July 1971; monthly samples were between 20 and 30 individuals.

The other area sampled in this study was at Guadalupe Island, Mexico, located approximately 200 km west of Punta Baja, Baja California. Collections were made along the protected east side of the island, concentrating on an area 3 km from the southern tip known as Lobster Camp (lat. 29°01′N, long. 118°14′W). Year-round sampling at Guadalupe Island was not possible, and the 130 individuals taken there were from three expeditions, January 1970 (16 specimens), April 1970 (53 specimens), and May 1971 (61 specimens).

Supplemental collections were made at La Jolla, Calif., including a sample of large individuals from a spearfishing meet on 19 July 1970.

The standard length of each fish was measured, and its coloration noted. Several dorsal spines were removed and frozen, and the gonads were fixed in bouin's fluid.

Age Determination Methods

Age determination by counting annular marks on the otoliths or scales was precluded in *P. pulchrum*. The otoliths are extremely small and difficult to locate, and the central portions of nearly all the scales were either clear or irregularly banded, indicating regeneration.

The bones and spines of *P. pulchrum* did show regular markings, and younger fish could be successfully aged by counting the marks on either the bones (opercula or cranial ridges) or the dorsal spines. However, the proximal portions of the bones tended to thicken and obscure the earlier marks on older California sheephead and only dorsal spine annuli could be used for age determination.

Dorsal spines were prepared as follows: the flesh was removed by means of a household enzyme product (Ossian 1970) and the spines were air dried. The classical methods of decalcification and/or thin sectioning (e.g., Cuerrier 1951) were not used. Instead, a high-speed grinding tool with a thin abrasive disc was used to cut cleanly through the spine at a point just distal to the swollen portion of the base. The spinous portion was then thrust through an opaque light shield so that only the cut base protruded. A strong microscope light was directed to the lower portion of the shield so that the only light visible on the other side then came through the projecting base of the spine. The hyaline layers of the spine transmit much more light and the illuminated pattern, resembling tree rings, is easily seen in a dissecting microscope.

The second dorsal spine was used for primary counts; the ring patterns on the other spines were identical, and were used to verify counts for individuals. Counts on each spine were made by two people and were used in the analysis of growth only when they agreed. False rings, probably caused by abnormal growth conditions, were identifiable in young individuals by their proximity to other annuli and their tendency to be incomplete.

Rarely, older fish showed a marked degeneration of the central portion of the spine, which became hollow and oil-filled, making age determination from spines impossible.

A series of measurements of 100 spines was made with an ocular micrometer at a magnification of 30×. At this magnification, one ocular micrometer unit equals 0.033 mm. The radius was measured at midspine on a line perpendicular to and beginning at the indentation axis. Distances from the center of the spine to each annulus were recorded for back calculation of length, along the radius line. Finally, the distance from the spine margin to the outermost annulus was measured for determination of the time of annulus formation.

Methods of Reproductive Biology

In the laboratory, each gonad was blotted dry, weighed, and a segment of one lobe was dehydrated in alcohol and embedded in paraffin. Slides were prepared of cross-sections of the lobe, cut at thicknesses of 5, 10, and 25 μm; thicker sections have less tendency to collapse and were made to ensure that the overall configuration of the cross-section could be observed. Sections were stained with ehrlich's hematoxylin and eosin.

Each gonad was classified according to sex and state of development. Assignment of a developmental class depended on the predominate stage of gametogenesis seen in the gonad. The division of gametogenic stages is as follows:

Oogenesis was divided into five stages, following criteria detailed for a variety of species by Kraft and Peters (1963). Smith (1965), and Moe (1969).

Stage 1. Very small (15-30 μm in diameter) oocytes with a large nucleus, single nucleolus, and a relatively small amount of basophilic cytoplasm.

Stage 2. (30-50 μm) Previtellogenic oocytes with a strongly basophilic cytoplasm and multiple nucleoli around the nucleus margin.

Stage 3. (150-300 μm) Vitellogenesis begins with the deposition of yolk vesicles in the less darkly staining cytoplasm. A thin zona radiata can be seen in late stage 3.

Stage 4. (280-450 μm) Cytoplasm filled with yolk vesicles and globules; the zona radiata well developed and strongly acidophilic.

Stage 5. (450-1,050 μm) Mature or nearly mature oocytes, uniform in appearance due to the coalescence of the yolk globules. The nucleus is eccentric and the zona radiata is thin and nonstriated. These oocytes are often extremely irregular in outline and Roede (1972), who noted the same irregularity in mature eggs of other labrids, probably correctly attributed this to distortion during fixation and staining. This stage was seldom seen, but several specimens were seen with eggs in the ovarian lumen and stage 5 oocytes still within the follicle.

Spermatogenesis occurs in small crypts, in which all the cells are at the same stage. The development and appearance of the spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and mature sperm follows very closely the descriptions given by Hyder (1969) for *Tilapia* and by Moe (1969) for *Epinephelus morio*, and will not be repeated here.

The gonadal development classes, intended to parallel those of Moe (1969) and Smith (1965), were designated as follows:

Class 1. Immature female. Stages 1 and 2 oocytes present, atretic or brown bodies (Chan et al. 1967) absent. The ovarian lamellae are pressed closely together and the lumen is small.

Class 2. Resting mature female. Oocyte stages 1, 2, and 3 present, with stage 2 predominating. Atretic bodies are usually present.

Class 3. Active mature female. Oocyte stages 3 and 4 predominate in the lamellae. In late class 3, stage 5 oocytes are also present.

Class 4. Postspawning female. Ovary is disrupted, with many empty follicles in the lamellae. Some degenerating stages 4 and 5 oocytes are usually found in the lamellae and lumen, respectively.

Class 5. Transitional. Seminiferous crypts begin to proliferate in the lamellae, but some stage 2 oocytes can be seen. These oocytes degenerate and decrease in number as spermatogenic activity begins to dominate the gonad.

Class 6. Inactive male. Crypts containing primary and secondary spermatocytes predominate; few spermatids and mature sperm are seen.

Class 7. Active male. Spermatids and tailed sperm increase in abundance until, in the ripe phase, sperm are densely packed in the collecting ducts and many crypts have coalesced.

Class 8. Postspawning male. Ducts are still expanded, but few sperm can be seen in them. Many new crypts containing spermatogonia are present. This apparently is a short-lived stage that rapidly gives way to the resting (class 6) testis.

Fecundity determinations were made by count-

ing yolky oocytes. A thick cross-section of the ovary was cut from near the middle of the lobe, weighed, and then agitated to dislodge as many oocytes as possible from the ovarian lamellae. Oocytes remaining in the lamellae were teased out so that a complete count could be made. An estimate of the number of yolky oocytes per gram of ovary could then be made directly from the sample. The total number of eggs in the ovary was then approximated by multiplying by the total weight of the ovary.

Relative abundance of coloration types was estimated directly from field observations. To eliminate the effects of any differential depth distribution, visual transects were either run perpendicular to depth contours or were compiled from a series of equal length runs parallel to successive contours. Transects were approximately 50 m in length. The number of California sheephead in each color phase was recorded. It was assumed that both coloration types are equally visible, and this is probably valid. California sheephead are not secretive when adults; only juveniles tend to remain close to cover. Larger males appear warier than other individuals, but still remain in sight. The problem in observing California sheephead is not in avoidance, but inquisitiveness. Occasionally transects had to be aborted because of the tendency of *Pimelometopon* to follow the diver.

RESULTS

Age and Growth

Van Oosten (1929) set forth criteria for the acceptance of annuli on scales or bones as yearly marks. These criteria apply equally well to spines, and are as follows: (1) The spine must remain constant in identity and grow proportionally with the fish. (2) Only one mark must be formed each year. (3) The body lengths calculated by using prior annuli on the spine (back-calculated lengths) should agree with the actual lengths of younger age groups.

The criteria will be discussed in order.

(1) Dorsal spines were certainly constantly identifiable in all individuals of *P. pulchrum* examined. The relationship of spine radius to standard length (Figure 1) is satisfactorily expressed in a linear fashion ($r = 0.787$) and there is no apparent indication of allometric growth of the spine, at least for fishes of lengths greater than 130 mm. Much of the scatter in the data is due to variability in the location of the cut made across the tapering spine.

(2) The increment of distance from the last annulus to the outer edge of the spine should increase with the time since the formation of that mark. If one mark is formed each year at a particular time, the average marginal increment should drop to near zero at the time of annulus formation, then steadily increase for the rest of the year. This pattern is shown (Figure 2) for 77 California sheephead from Catalina taken throughout the year. Successive age groups did not differ in time of annulus formation, so the data are combined for all aged fish. The distinct hyaline bands appeared to be formed in June and July, at the beginning of the period of warming water in the Catalina area (Quast 1968). Formation of growth marks has been found to occur in other inshore California fishes at a similar time (Joseph 1962; Norris 1963; Clarke 1970). Ring formation also overlaps with the initiation of reproductive activity, although egg production and spawning continue well into September (see below).

(3) Lengths of *P. pulchrum* at previous ages were calculated by a modified direct-propor-

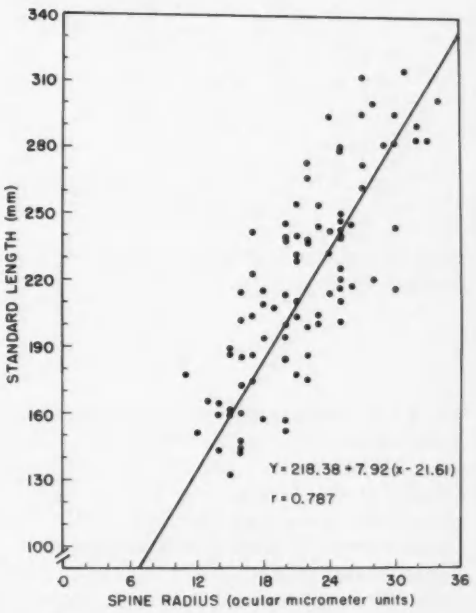

FIGURE 1.—The relationship of dorsal spine radius to standard length for 117 specimens of *Pimelometopon pulchrum* from Catalina Island. One ocular micrometer unit equals 0.033 mm at 30×.

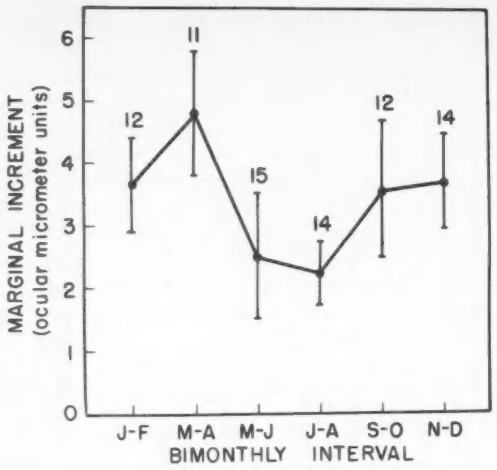

FIGURE 2.—Mean marginal increments for six bimonthly intervals from 78 specimens of *Pimelometopon pulchrum* from Catalina Island. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point.

Table 1 shows the back-calculated lengths for 100 California sheephead from Catalina over eight age groups, derived from spine radius measurements. The means from back calculation are also given in Figure 3 for comparison with empirical data. The mean standard lengths for each age (Figure 3) demonstrate good agreement with the back-calculated data.

There appears to be a slight slowing of growth after the fourth year in the Catalina California sheephead population. This may reflect the onset of a diversion of a significant amount of energy into egg production, since most 4-yr-old fish examined were mature females (see below). A second period of more rapid growth is suggested after the seventh year, at an age where many of the Catalina California sheephead are beginning to transform from female to male. There is no evidence for a decrease in the rate of growth up to age 13, where the average standard length is 470 mm. *Pimelometopon pulchrum* is quite capable of growing larger than this, and some individuals have very long lifespans. Fitch and Lavenberg (1971) mention a 32-inch (815-mm) male aged at 53 yr, and an 8.3-kg female, no length given, that was 30 yr old. Although exact age determination becomes difficult for large and old individuals, it is occasionally possible. The largest California sheephead encountered in this study were a 592 mm SL male, 20 yr of age, and a 538 mm SL male which had lived 18 yr. Size-age distributions can vary for different locations. In a sample taken by the California Department of Fish and Game at a spearfishing meet at San Pedro, Calif., on 28 March 1971, the mean standard length for males was 661 mm (range 545-745 mm) and for females was 450 mm (range 294-656 mm).

The pattern at Guadalupe Island is different from that at Catalina (Figure 4). While the sample

TABLE 1.—Back-calculated lengths for age groups 1 through 8 of *Pimelometopon pulchrum* from Catalina Island.

Age group	N	Mean length of subsample (mm)	Mean length of total sample (mm)	Back-calculated lengths (mm) for ages 1	2	3	4	5	6	7	8
1	8	100	116	97							
2	16	158	155	100	127						
3	22	198	197	106	139	168					
4	17	231	238	124	152	178	200				
5	11	246	245	130	164	185	203	225			
6	11	266	272	129	159	191	212	230	251		
7	7	289	294	128	163	190	225	247	274	295	
8	8	359	368	145	183	220	254	279	299	320	343
Overall means of calculated lengths				117	150	184	214	242	272	308	343
Number of individuals				100	92	76	54	37	26	15	8

tionality method given by Rounsefell and Everhart (1953) as follows:

$$\frac{L' - C}{L - C} = \frac{S'}{S}$$

where L = length of the fish at the time the spine was obtained, L' = length at the time a particular annulus was formed, S = total length of the spine radius, and S' = length along the spine radius to the annulus in question. The term C is a factor used to correct for the length obtained before the spine was formed, and is estimated by the intercept of the length axis on a fish length versus spine radius plot (Figure 1). In the case of the Catalina California sheephead population, C was equal to 47.2 mm.

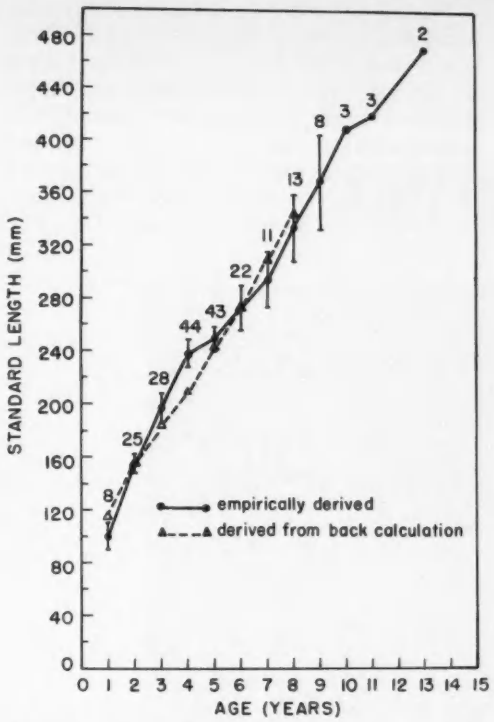

FIGURE 3.—Mean standard length versus age in the Catalina population of *Pimelometopon pulchrum*. Sample sizes are shown for each interval, and 95% confidence limits for the mean are drawn on either side of each point. Means for back-calculated lengths are shown for comparison.

is smaller and more variable than that from Catalina, a marked tendency towards dwarfing is clear. Judging from the mean lengths of each age class, the Guadalupe California sheephead complete their first year of growth at a standard length about 20 mm shorter than those at Catalina. For each of the next 3 yr they fall behind an additional 10 mm, after which relative growth slows even more. By the eighth year, the mean standard length of Guadalupe California sheephead is a full 100 mm less than that found at Catalina.

In spite of the dwarfing, the Guadalupe population shows some interesting parallels with Catalina. The slowing of the average rate of growth at the time of maturity (age four) is more striking here, and growth appears to pick up again after the sixth year, by which time at Guadalupe most individuals are males (see below). This suggests that an increase in the growth rate is associated with sex changes, a topic covered more fully in the discussion. In the Catalina population, both the increase in growth rate and the maximum number of sex changes occur about a year later than in the Guadalupe population.

Anatomical Features of the Gonad and Sexual Transformation

The gonad of *P. pulchrum* consists of two hollow sacs in the extreme dorsal part of the body cavity. Genital arteries and veins run through the dorsal part of each lobe, giving off segmental branches. The wall of each lobe consists of connective tissue and smooth muscle.

The internal structure is made up of germinal epithelium in a series of folds or ridges, the gonadal lamellae. These are numerous in the female, but few in the male. There is a small

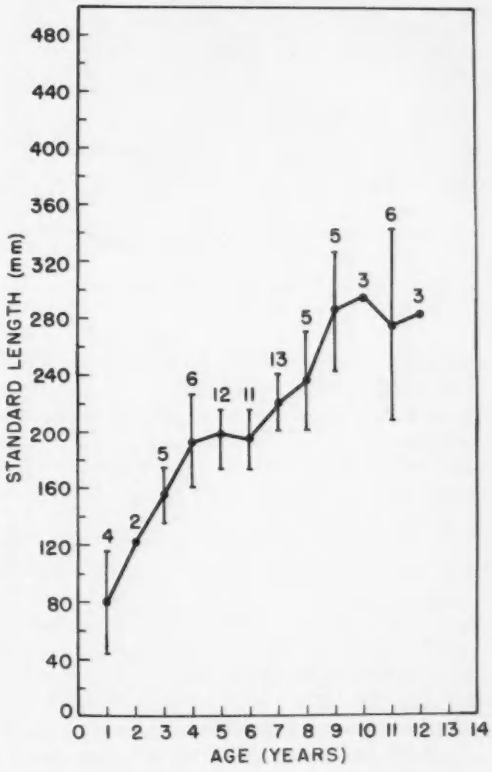

FIGURE 4.—Mean standard length versus age in the Guadalupe Island population of *Pimelometopon pulchrum*. Sample sizes are shown for each age, and 95% confidence limits are drawn on either side of each point.

alamellar portion in the most ventral section of the gonad, similar to that described by Smith (1965) for some serranids.

In the female, oogenesis takes place within the lamellae. When the egg ripens, it breaks into the central lumen, which leads to the common oviduct. Some oocytes are interrupted in their normal development and undergo a degeneration into various types of corpora atretica (Figure 5). These have been described briefly for serranids by Smith (1965) and in detail for *Monopterus albus* by Chan et al. (1967). Chan and his colleagues discuss the possible endocrine function of atretic structures, and state that all types of corpora atretica eventually end up as brown or yellowish bodies which are long lasting in the gonad. In *P. pulchrum*, brown bodies can usually be found near the gonad wall and in the central portion of the lamellae. Judging from the number of these terminal phase corpora atretica in resting (class 2) females compared with the usually greater number of earlier stage atretics (Chan et al. 1967) in postspawning females, the brown bodies are probably formed from more than one degenerating oocyte.

Brown bodies are also found in male gonads; some of these are almost certainly the result of oocyte degeneration in the previous female phase (Figure 6), while others may be the result of degeneration and coalescence of unshed sperm.

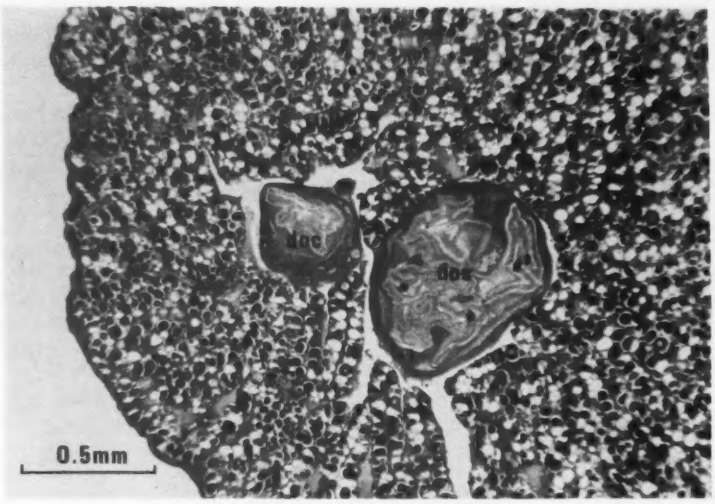

FIGURE 5.—Degenerating oocytes (doc) in the lumen of a resting ovary of *Pimelometopon pulchrum*. Specimen number PP411, 217 mm SL.

During sexual transformation, crypts of developing spermatocytes appear, first at the base of the ovarian lamellae, and then throughout the gonad (Figure 7). Unshed eggs and nonvitellogenic (stage 2) oocytes are gradually reabsorbed and the number of lamellae visible in cross-section are reduced. The basic structure of the gonad remains ovarian, with a central lumen into which the lamellae protrude. The lumen however no longer functions in gamete transport and sperm are collected in a series of sinuses on the periphery of the gonad, reaching the outside by means of ducts in the wall of the now unused oviduct. This is very similar to the anatomy described by Reinboth (1962, 1970) for other labrid secondary (sex-reversed) males. No testes of the primary type were seen.

Transformation Schedule

To illuminate the life history patterns of the California sheephead populations, the gonad development classes were grouped in the following way:

Immature: Class 1 only.
Female: Classes 2, 3, and 4.
Transitional: Class 5 only.
Male: Classes 6, 7, and 8.

The distribution of sexual types by standard

length for *P. pulchrum* from Catalina Island (Table 2) and Guadalupe Island (Table 3), as well as the relative frequencies for each size grouping (Figure 8), are similar in both localities in that the small size classes are made up exclusively of immature females. Mature females are most abundant in the next size classes, and then become less numerous as males begin to predominate in the

FIGURE 6.–Degenerating oocytes (doc) in the lumen (l) and lamellae (la) of the gonad of a transitional individual of *Pimelometopon pulchrum*. Specimen number PP405, 317 mm SL.

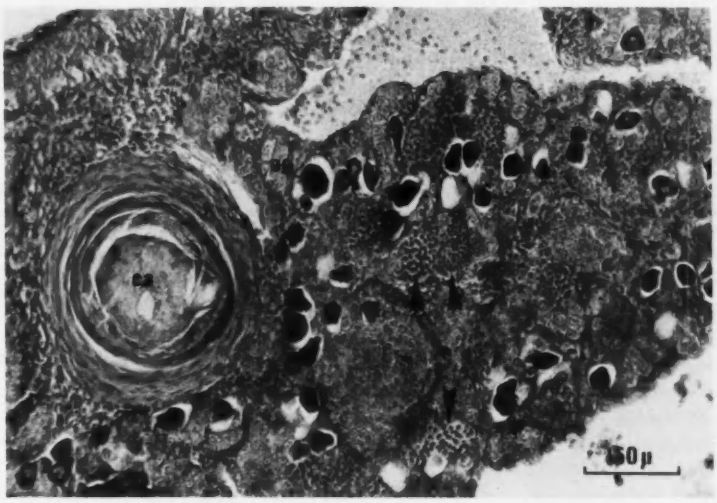

FIGURE 7.–Spermatogenic crypts (shown by arrows) developing in a gonadal lamella of a transforming *Pimelometopon pulchrum*. Stage 2 oocytes (oc) and a corpus atreticum (ca) can also be seen. Specimen number PP405, 317 mm SL.

TABLE 2.–Frequency of sexual types in each 20-mm size class for the Catalina Island population of *Pimelometopon pulchrum*.

Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
< 100	7	7	0	0	0
100-119	5	5	0	0	0
120-139	6	6	0	0	0
140-159	28	28	0	0	0
160-179	18	18	0	0	0
180-199	25	24	1	0	0
200-219	34	15	19	0	0
220-239	40	6	33	0	1
240-259	49	2	39	5	3
260-279	33	0	25	4	4
280-299	23	0	15	2	6
300-319	14	0	9	1	4
320-339	10	0	3	0	7
340-359	16	0	5	0	11
360-379	9	0	1	0	8
380-399	7	0	2	0	5
> 400	17	0	1	0	16
Totals	341	111	153	12	65

TABLE 3.–Frequency of sexual types in each 20-mm size class for the Guadalupe Island population of *Pimelometopon pulchrum*.

Standard length (mm)	Number of fish	Immature	Mature female	Transitional	Mature Male
< 100	5	5	0	0	0
100-119	5	5	0	0	0
120-139	3	3	0	0	0
140-159	8	1	7	0	0
160-179	12	0	9	0	3
180-199	15	0	10	0	5
200-219	16	0	5	1	10
220-239	11	0	2	1	8
240-259	16	0	4	2	10
260-279	10	0	2	2	6
280-299	6	0	1	0	5
300-319	7	0	1	0	6
320-339	7	0	1	0	6
340-359	2	0	0	0	2
360-379	3	0	0	0	3
380-399	1	0	0	0	1
> 400	3	0	0	0	3
Totals	130	14	42	6	68

largest sizes. Transitionals were found in intermediate sizes, in numbers which varied seasonally (see below).

At Catalina, most California sheephead mature at standard lengths between 190 and 230 mm. Sexual transformation occurs over a broader size range beginning at 250 mm, with a peak of activity apparently occurring at standard lengths between 310 and 330 mm.

The dwarfing phenomenon found in the Guadalupe population is again evident (Table 3, Figure 8). Maturity begins at a length near 140 mm, and the majority of individuals are male by a length of 210 mm. Peak transformation activity appears to occur in the population in fishes ranging from 190 to 230 mm in standard length.

The actual time courses for all these events become evident when the relative frequencies of

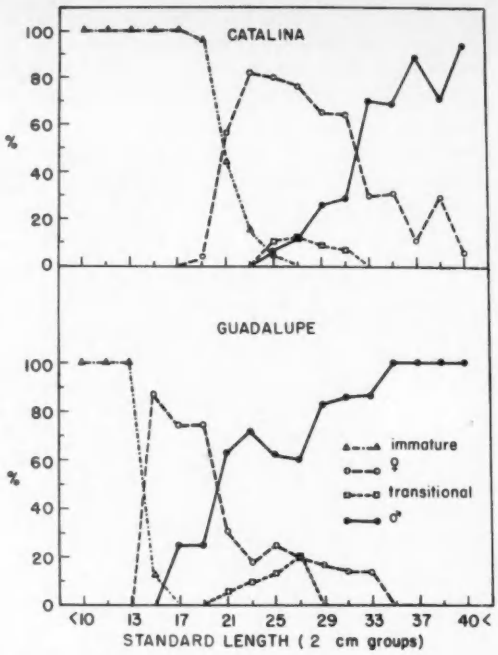

FIGURE 8.–Proportions of each sexual type in successive 2 cm standard length groupings for the Catalina Island (top) and Guadalupe Island (bottom) populations of *Pimelometopon pulchrum*.

TABLE 4.–Frequency of sexual types in each year class of *Pimelometopon pulchrum*.

	Age class	Number of fish	Immature	Mature female	Transitional	Mature male
Catalina population	1	7	7	0	0	0
	2	33	33	0	0	0
	3	34	34	0	0	0
	4	42	5	35	1	1
	5	40	0	33	2	5
	6	27	0	16	3	8
	7	15	0	9	1	5
	8	14	0	4	0	10
	9	8	0	2	0	6
	10+	8	0	1	0	7
Totals		228	79	100	7	42
Guadalupe population	1	4	4	0	0	0
	2	2	2	0	0	0
	3	5	5	0	0	0
	4	4	0	4	0	0
	5	10	0	5	1	4
	6	13	0	7	0	6
	7	14	0	2	3	9
	8	9	0	2	0	7
	9	6	0	0	1	5
	10+	13	0	3	0	10
Totals		80	11	23	5	41

the sexual types in each age class are graphed (Figure 9). The curves are based on the frequency distributions listed in Table 4.

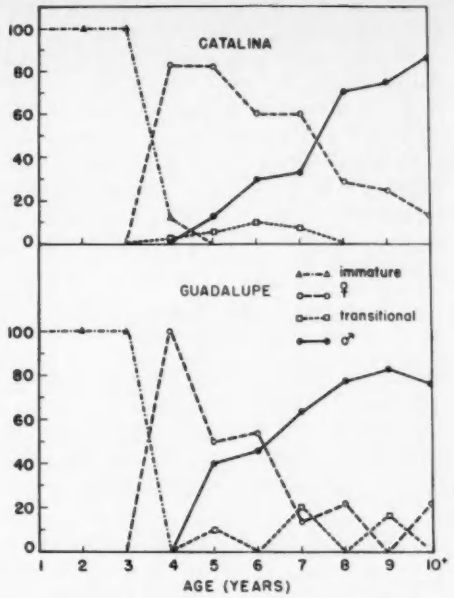

FIGURE 9.—Proportions of sexual types in each year class of *Pimelometopon pulchrum* from Catalina Island (top) and Guadalupe Island (bottom). The last age grouping consists of all fishes 10 or more years old.

In both populations, sexual maturity begins in the fourth year of life for virtually all members. By using age groupings, the skewness introduced by the dwarfing at Guadalupe is removed, and differences in the transformation activity time schedule in the two populations are revealed. At Guadalupe, males are present in essentially the same abundance as females in age classes 5 and 6, and strongly predominate at age 7 and thereafter. Therefore the majority of California sheephead at Guadalupe Island spend no more than 2 or 3 yr as functional females.

Transformation generally occurs later in the Catalina population. Most individuals are functional females for at least 4 yr, and males predominate only after age 8.

Distribution of Gonad Development Classes with Time

The active state of gonads may be determined directly through histological examination or inferred from the appearance and the size of gonad (gonad indices).

The seasonal distribution of mature gonad development classes for 166 California sheephead from Catalina is shown in Figure 10. As expected, immature fishes, which are not shown in the Figure, occur throughout the year. Resting stage females (class 2) were encountered from August through May, and predominated from October to April. Active females (class 3) were present May

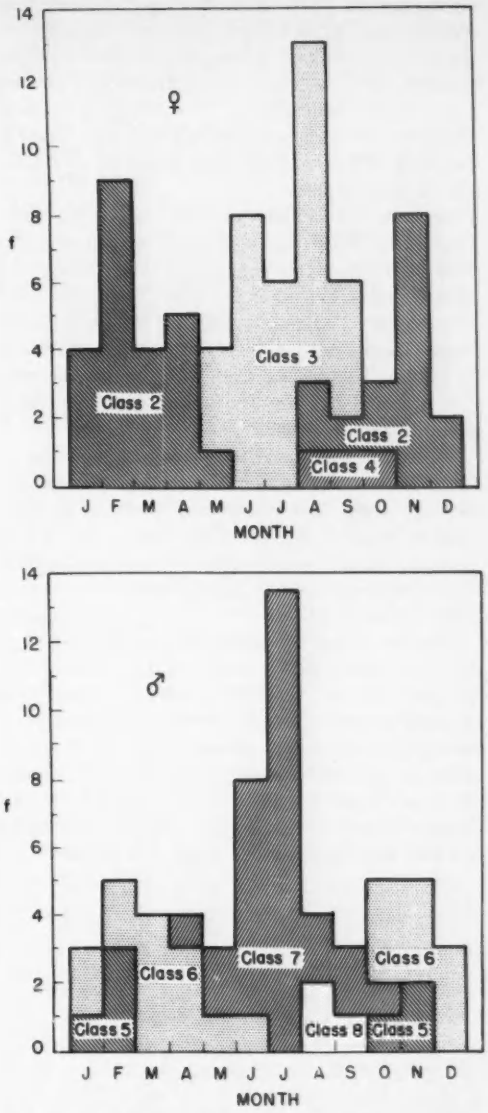

FIGURE 10.—Number of individuals of *Pimelometopon pulchrum* in each mature gonadal development class from monthly samples taken at Catalina Island.

through September. Late class 3 gonads were seen in July, August, and September, and most spawning activity probably takes place in these months. Females with postspawning ovaries (class 4) were captured in low numbers from August to early October. Class 4 appears short-lived, quickly receding into a resting class (class 2) or transitional (class 5) phase.

Transitional individuals were found only from October to March at Catalina. Those taken in October and November were all in the early stages of transformation, with many stage 2 oocytes and a few scattered spermatogenic crypts in evidence. Transitionals captured in February at Catalina or in May at Guadalupe were more advanced, with few stage 2 oocytes and spermatogenic crypts dominating the gonad.

Most males at Catalina were inactive (class 6) from October through April, closely paralleling the period seen for females. Active gonads predominated in samples from fish taken in May through September. Again the pattern suggests that spawning activity takes place from August through early October.

Further support for designating this period as the spawning season comes from the gonad indices (Figure 11) of Catalina females caught in different months. These reflect a similar pattern seen in the analysis of gonad development states. After a quiescent period from October through April, the ovaries begin to increase in size until a maximum is reached in June and July. Spawning reduces the average index steadily from then until September. The resting value is then seen again, remaining constant through the winter.

The index used was gonad weight scaled to compensate for different lengths of individuals. When only the mature females less than 310 mm in standard length are included in the analysis, the relationship between gonad weight and standard weight is sufficiently linear (Pearson correlation coefficient = 0.845 [$P < 0.001$] on 24 individuals caught in June) that the use of the following formula is justified:

$$\text{Gonad index} = \frac{(\text{gonad weight in grams})\,(100)}{(\text{standard length in mm})}$$

The size range used includes the great majority of reproductive females at Catalina.

An analysis of the spawning season of *P. pulchrum* at Guadalupe Island was not possible due to the lack of year-round sampling.

Multiple Spawning and Fecundity

Two or more distinct groups of ripening oocytes were usually apparent in the ovaries of *P. pulchrum* examined in June and July. The size distribution of yolky oocytes in an ovarian cross-section (Figure 12) from a female, 244 mm SL, captured at Catalina in mid-July, shows that there is one group of eggs ready to be spawned, and that two other distinct groups are undergoing vitellogenesis. This type of successive maturation of several groups of oocytes is termed asynchrony, and is characteristic of species that have comparatively long breeding seasons and multiple spawnings by individuals within each season (Yamamoto and Yamazaki 1961).

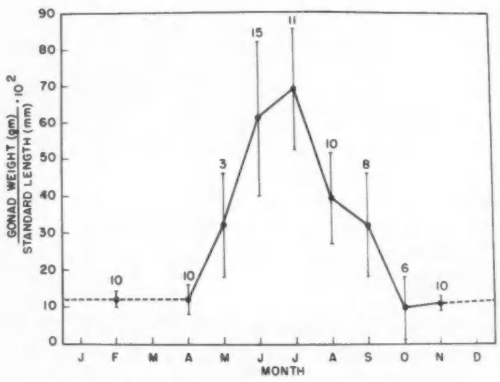

FIGURE 11.—Average gonad indices for monthly samples of mature female *Pimelometopon pulchrum*, all of standard lengths less than 300 mm. Sample sizes are shown above the bracketed lines, which are the 95% confidence limits of the mean.

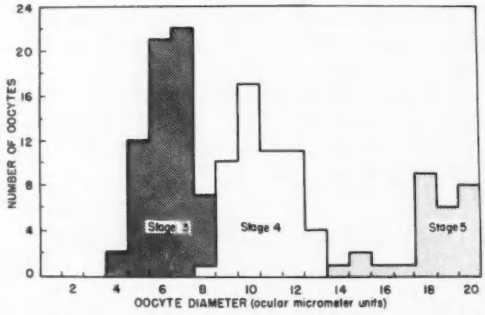

FIGURE 12.—Size distribution of yolky oocytes in an ovarian cross-section of a 244 mm SL female of *Pimelometopon pulchrum* captured 22 July at Catalina Island. The oocytes are also classified according to their degree of development.

Further evidence for multiple spawning is seen in the ovaries from some females captured in August and early September. There were a few mature eggs free in the lumen and numerous empty follicles in the lamellae, both indications of recent spawning. At the same time, another group of vitellogenic oocytes were observed developing in the lamellae and these would presumably have been spawned at a later time.

As Yamamoto and Yamazaki (1961) point out, the presence of multiple spawning complicates any determination of the number of eggs produced each year by an individual fish. Estimates can be made from an analysis over time of frequencies of egg diameters, such as that done by Clark (1934) for *Sardinops caerula*. Such analyses require a large sample over the mature size range and this was not available for *P. pulchrum*.

Counts of the yolky oocytes in subsamples of ovaries made for California sheephead females captured in July (Table 5) are probably overestimates of the number of eggs spawned during the season. This is because, as pointed out above, the relationship between the number of these oocytes and the number actually spawned depends on the survival rate of the oocytes to maturity and the proportion that are actually ejected from the body. The smaller numbers of stage 5 oocytes relative to stages 3 and 4 (Figure 12) indicates a loss during development. There are certainly some eggs left in the lumen of postspawning females. These degenerate and are presumably absorbed during the resting phase.

TABLE 5.–Estimates of the total number of vitellogenic oocytes and density of those oocytes in the ovaries of *Pimelometopon pulchrum* captured at Catalina Island in July 1970.

Standard length (mm)	Date of capture	Weight of ovary (g)	Estimated number of yolky oocytes, total	Estimated number of yolky oocytes per gram of ovary
209	7/24	6.87	36,068	5,250
235	7/22	16.69	74,270	4,450
238	7/22	16.53	76,870	4,650
254	7/19	28.00	171,500	6,125
280	7/22	17.23	88,300	5,125
311	7/19	50.02	296,600	5,930
314	7/19	19.80	113,850	5,750
330	7/19	34.07	167,600	4,920
359	7/19	41.63	258,100	6,200

Mean and 95% confidence limits of oocyte density, oocytes per gram = 5,377 ± 499.

For an analysis of the functional significance of sequential hermaphroditism, actual egg numbers are less important than data on the relative values for age- or size-specific fecundities (Williams 1966; Warner in press). As long as the number of eggs per unit weight of ovary does not vary appreciably with size or age, weights of active prespawning ovaries can be used to represent relative fecundities. The last column of Table 5 shows there is no apparent effect of fish length on egg density within the ovary.

Comparison of ovary weights and standard lengths for mature females captured at Catalina in June and July (Figure 13) shows that fecundity increases exponentially with the length. The exponential equation:

$$W = 1.31 \times 10^{-3} L^{2.95}$$

(W = gonad weight, L = standard length) indicates that the increase of gonad weight with

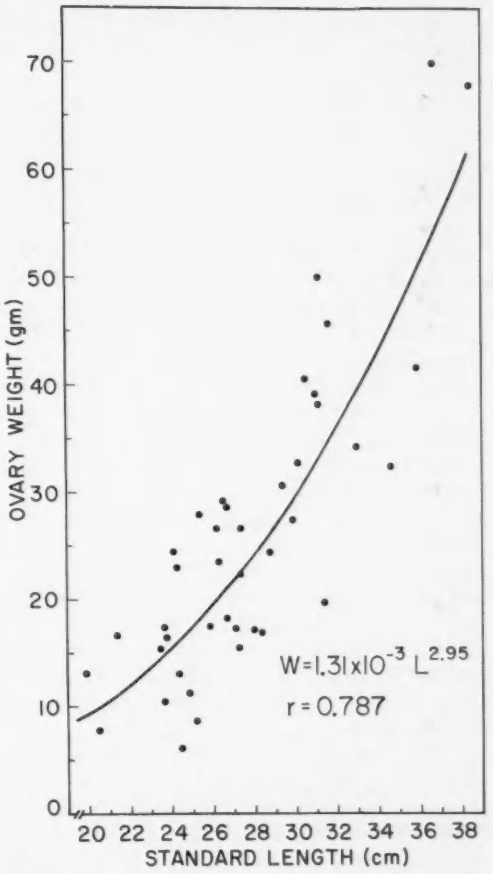

FIGURE 13.–Ovary weight versus standard length for females of *Pimelometopon pulchrum* captured in June and July at Catalina Island.

length conforms to a simple cube law relationship, which would be expected if gonad weight remains some constant proportion of the total weight. The exponent 2.95 was determined by a least-squares regression fit to a logarithmic transformation of the data. The confidence limits around the regression line become increasingly large with higher values of W and L, and the curve should not be used for extrapolations beyond the range of the data. Ovary weights in relation to age are shown in Figure 14. There are few data for the older age classes, but there is a definite positive correlation of the fecundity and the age of the individual.

Coloration, Sex, and Field Distribution of Coloration Types

The California sheephead is found in three main color phases (Crozier 1966), all of which are closely correlated with sexual state.

For the first year, *P. pulchrum* has juvenile coloration, a gold or salmon body color with black spots on the anal fin, the anterior and posterior portions of the dorsal fins, and on the caudal peduncle, and with a silver lateral stripe extending from the eye to the caudal fin. Crozier (1966) stated that the initial body color was gold, and this was gradually replaced by the reddish adult shade. The juvenile coloration was seldom seen in individuals over 100 mm SL, and has never been found in sexually mature individuals.

The most common color pattern of *P. pulchrum* is a uniform rose or salmon color, covering the entire body with the exception of the chin, which is usually white in mature individuals. The median and pelvic fins are darker than the body, ranging from dusky red to black. The pectoral fins usually match body color. Uniform coloration may be obscured by a melanistic condition which causes the entire body to appear brown. This occurs in varying degrees, making the fish appear almost black in extreme cases. Eleven percent of the uniformly colored fish captured at Catalina were designated melanistic, as were one-third of all uniform types at Guadalupe.

A uniform coloration is characteristic of immature fish as well as mature females. Histological analysis indicated, however, that the relationship was not perfect. At Catalina, 3.5% of the individuals designated uniform in color were discovered to have male gonads. When only sexually mature uniformly colored California sheephead were tallied, 5.1% were male. These males ranged

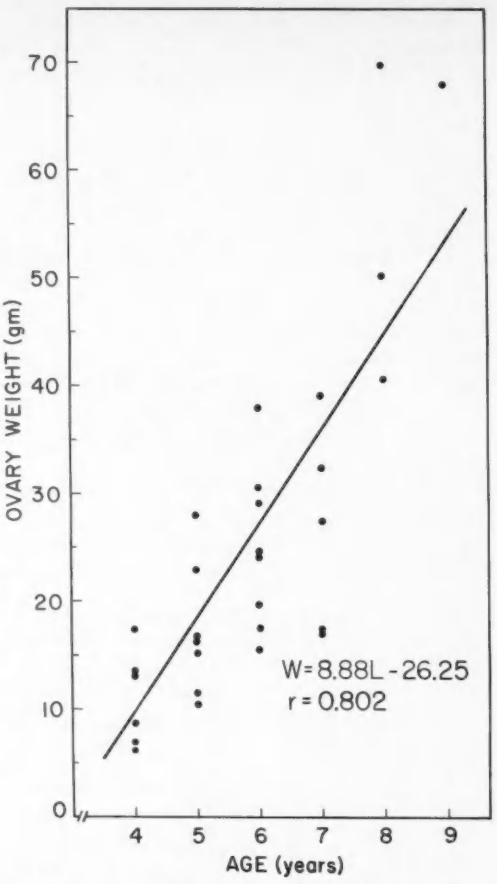

FIGURE 14.–Ovary weight versus age for females of *Pimelometopon pulchrum* captured in June and July at Catalina Island.

in length from 245 to 315 mm. and were captured in June, July, and December. Examination of a large series of gonad cross-sections from these individuals revealed a few stage 2 oocytes within the lamellae from two captured in July. This can be taken as evidence for a recent sex change. All the others had gonads of completely normal male appearance.

Field notes revealed that all of these individuals were melanistic, and 70% were recorded as having some male external characteristics, such as a small nuchal hump or slight differential darkenings of either the head or tail regions (see below). This suggests the possibility that some of these individuals may have been incorrectly typed due to the ground color being obscured by melanin.

Males in uniform coloration are more frequent in the Guadalupe population. A total of 6 out of 57 (10.5%) uniformly colored individuals were males. Elimination of immature fish from the count raises the figure to 12.3% males. Four of the six were melanistic, one of these with slight male characteristics. The other two individuals possessed normal uniform coloration with no darkening.

In the third color phase the head region, including the opercle, is dark brown or black. The chin remains white, and the midsection retains the reddish hue of the uniform type. The caudal portion, beginning approximately on a line connecting the initial soft rays of the dorsal fin with the anterior limit of the anal fin, is also dark brown or black. The median fins and pelvics remain generally dark in color, and the pectorals may acquire a dark band at their tips.

This coloration is found exclusively in males and some transitionals (see below). It is usually accompanied by two other male secondary sexual features common in the Bodianinae, the nuchal hump and filamentous extensions of the median fins. The hump appears to increase in relative size as the male gets larger, making the head appear increasingly angular in profile. No individual with this bicolored pattern was found to have functional ovaries. During the breeding season, the pattern serves as an excellent indicator of a functional male.

Individuals classified as transitional varied in coloration. Of 11 transforming California sheephead for which coloration records exist, 3 were scored uniform in color and 2 as bicolored. The remaining 6 were recorded as intermediate in coloration, usually involving a slight darkening of the head, caudal region, or both. The three uniform individuals were classed as early transitionals (large amounts of stage 2 oocytes still in the gonad); the two bicolored fishes were classed as late transitionals (only a few degenerating oocytes in the gonad cross-sections).

The distribution of uniform and bicolored types in field populations, determined by visual transects (Table 6) shows that bicolored males are present in remarkably similar proportions in both localities, occurring in a ratio of about 5.5 uniform individuals to every bicolored individual. Confidence limits for estimating the proportion of bicolored individuals were calculated from a binomial distribution, $n = 216$ and 407 for Catalina Island and Guadalupe Island, respectively (Dixon and Massey 1969).

TABLE 6.—Numbers of coloration types in two populations of *Pimelometopon pulchrum*, determined by a series of visual transects.

Locality	No. of transects	No. of uniform type	No. of bicolored type	Proportion p of bicolored types and 95% conf. limit
Catalina Island	70	183	33	0.153 ± 0.048
Guadalupe Island	93	343	64	0.157 ± 0.035

DISCUSSION

Anatomical Features of the Gonad and Sexual Transformation

The ovary of *P. pulchrum* is essentially identical with that of the labrid *Coris julis*, which was studied in detail by Reinboth (1962). Reinboth, however, did distinguish between the testes of those *C. julis* born as males (primary males) and those that become males through sex reversal (secondary males). In the former, the testis appears rather solid and flattened, and sperm are transported by means of a single vas deferens in each lobe. The secondary male has a testis like that described here for *P. pulchrum*. The two types differ in the structure of the vas deferens posterior to the gonadal lobes, which surrounds the old oviduct in secondary males, but is a simple tube in primary males (Reinboth 1970).

When primary and secondary males are present in a single species, Reinboth (1970) termed the species diandric. When only secondary males are present, the species is termed monandric. To Reinboth's (1970) list of monandric species (*Labrus turdus*, *L. merula*, *L. bergytta*, *Hemipteronotus novacula*, and possibly *L. bimaculatus*) we may add *P. pulchrum*. Other labrid species have been studied without regard for the primary-secondary male phenomenon (Atz 1964; Reinboth 1970), and cannot be categorized with certainty as monandric or diandric.

The transition from a functional ovary to a testis has been described in detail for labrid fishes in both naturally occurring situations (Reinboth 1962; Sordi 1962; Okada 1962; Roede 1972) and under the influence of hormone administration (Reinboth 1962, 1963; Roede 1972). These reports are essentially in agreement with the present observations on *P. pulchrum*. There is no evidence of synchronous hermaphroditism (Atz 1964:147) in the Labridae, but Robertson (1972) found spermatogenic crypts in the ovaries of 28 of 29 females of

Labroides dimidiatus, and 15 of these had crypts with sperm or spermatids. Thus, the possibility of encountering a synchronously hermaphroditic labrid species should not be ruled out.

Transformation Schedule

Pimelometopon pulchrum fits the general labrid pattern of size and sex distribution. No males were found smaller than 230 mm SL at Catalina Island, and none smaller than 150 mm at Guadalupe. The longer size classes (above 350 mm and 230 mm at Catalina and Guadalupe, respectively) contain mostly males.

Data for labrid sexuality are usually in the form of size frequency distributions of males and females within a species (Atz 1964; Remacle 1970; Roede 1972). Some of these studies have been confounded by the presence of two distinct color patterns, the investigators wrongly assuming strict sexual dichromatism (see below). An additional complication is the possibility of two different types of males being present in some species, usually with different life histories and behavior (Reinboth 1970). Both of these problems are eliminated by histological examinations of the gonad, which also reveals the presence of intersexual or transitional individuals.

The absence of males from the smaller size classes at least suggests protogyny. However, similar patterns can also result from samples of a species exhibiting differential growth rates for the sexes (e.g., see Strasburg 1970, for weight and sex distributions of blue marlin, *Makaira nigricans*), and this should be taken into consideration.

Fourteen of the fifteen labrid species either reviewed or dealt with originally by Roede (1972) had similar patterns of length-sex distribution. Females predominated in the smaller size classes, males in the larger. The proportion of males in the smaller sizes (usually associated with a particular color pattern; see below) varied from practically none in some species of *Halichoeres* and *Hemipteronotus* up to nearly 30% for *Stethojulis strigiventer* (Randall 1955). Males became increasingly common as length increased and the longest size classes consisted almost exclusively of males.

Species of the genus *Symphodus* (*Crenilabrus*) appeared to exhibit a different pattern, with nearly equal numbers of males and females in the small size classes (Sõljan 1930a, b). Remacle (1970) believed that sex reversal is a rare phenomenon in this genus.

Age determinations allow several more inferences about the sexual life history of a species. When few or no young males can be found, there is strong evidence for protogyny since the possibility of differential growth is eliminated. The rate of transformation in different age classes can be estimated, and this provides an idea of how long the average individual spends in different sexual phases. Finally, by comparing the distribution of sex versus length with sex versus the age of the individual, it may be possible to assign a more critical role to one or the other as a causative factor for sex reversal.

The age at first maturity (4 yr) does not differ for *P. pulchrum* at Catalina and Guadalupe Islands, but the distribution of sexual transformation with age differs markedly. Most individuals in both populations function at least 1 yr as females. At Guadalupe, many change sex after 1 yr, and most are males within 3 yr after maturing. Most sex reversals occur at Catalina between the seventh and eighth year, 4 yr after maturing as a female. Some individuals remain female for shorter or longer periods of time. The oldest female encountered in this study was 17 yr old.

The dwarfing phenomenon at Guadalupe, which should bring about a slower rate of increase of fecundity with age, would have enough effect to decrease the optimum age of transformation in that population when compared to the Catalina population. This will be discussed in detail elsewhere (Warner in press).

Lonnberg and Gustafson (1937) determined the ages of a series of specimens of *Labrus bimaculatus* (as *L. ossifagus*) which they correlated with sexual state. They found that sex reversal occurred in individuals from age seven onward, and was associated with a color change from red to blue-striped. Females were found in diminishing numbers up to age 18, mostly confined to the red phase. Males in the red phase ranged from around 3 to 7 yr old; blue-striped males got as old as 25.

Other protogynous teleosts which have been investigated regarding age of transformation show a variety of patterns in the distribution of sex reversal over their life-span. Liem (1963) demonstrated that sex transformation in the synbranchid rice eel *Monopterus albus* occurs mainly when individuals reach about 30 mo of age (about 35 cm in length). Few fishes in nature deviated from this pattern. Liem (1963) was able

to induce earlier transformations by starving the individuals. Moe (1969) has carefully worked out the age distribution of sex reversal in the serranid *Epinephelus morio*, and found a rather smooth period of transition from female to male over at least 5 yr (ages 5 to 10), at a rate of about 15% of the individuals in a year class reversing per year. In a less comprehensive survey, McErlean and Smith (1964) estimated that transformation occurred at age 10 or 11 in *Mycteroperca microlepis* (Serranidae), and speculated that the age of the fish had more effect on sex reversal than the length.

To determine the effect of individual size on sex transformation in *P. pulchrum*, mean lengths of males and females in each age class were compared (Figure 15). If length is closely related to sex reversal, one would expect males to be larger than females of the same age, and this was found in both the Catalina and Guadalupe populations. In every age grouping where sample size permitted statistical analysis, males tended to be larger than females. Five of the seven groups tested (one-sided t-test for difference in means) were significantly different at the 5% level or less, and the remaining two were significant at the 10% level.

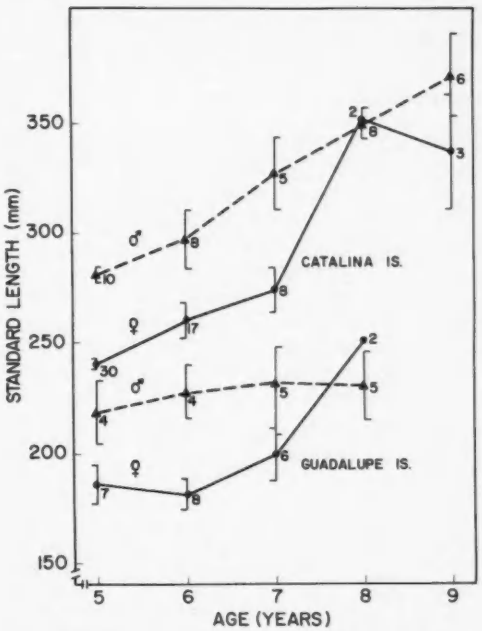

FIGURE 15.—Mean lengths for successive age classes of males and females of *Pimelometopon pulchrum*. Sample sizes are shown for each point, and standard error brackets are given when samples are large enough. For clarity, standard error brackets for males point to the right, and brackets for females point to the left.

An assessment of the effect of age on sex reversal was made in similar fashion, comparing the mean ages of males and females in successive size groupings (Figure 16). If sex reversal were closely related to the age of an individual, then males would tend to be older than females in a given length group. The relationship between age and sex is less strong (Figure 16). Sample sizes are not large, and the range of ages encountered in a sample is small relative to measured length values, so fewer significant results might be expected. Only one size group was found where males were significantly older than the females. However, the existence of several large negative t values in groups where the age of females is greater than that of males supports the idea that size is more important than age in effecting sex change.

The high average age of females in the larger size groupings of both populations (Figure 16) was not expected, and suggests that the individual growth rate may also be involved in sex reversal. The large separation between male and female mean ages begins with the 300-mm size grouping at Catalina, and the 200-mm group at Guadalupe. Inspection of Figure 8 reveals that at about these lengths, the proportions of males and females undergo an abrupt shift. A large percentage of the individuals in the populations apparently reverse sex at these sizes. Furthermore, the difference in ages between males and females of lengths above these "critical" sizes appears to be significant. The mean age of females larger than 300 mm at Catalina is 7.9, a full year older than males in the same size range ($t_{31} = 1.51$, $P<0.10$). Similarly, females larger than 200 mm at Guadalupe have a mean age of 9.5 yr, and males at that size range average 7.0 yr ($t_{32} = 2.80$, $P<0.001$). Thus the females that pass through the "critical" lengths without changing sex appear to be those individuals with relatively low rates of growth, suggesting both that slow growing individuals tend to be refractory to sex change, and that fishes with high rates of growth change sex more readily. The data of Figure 15 support this idea, as males are faster growing (larger) members of each age class. A check of the back-calculation information revealed that the growth rates of the large females were consistently low throughout their lifetime, and those of the small males had been high relative to other members of the age class.

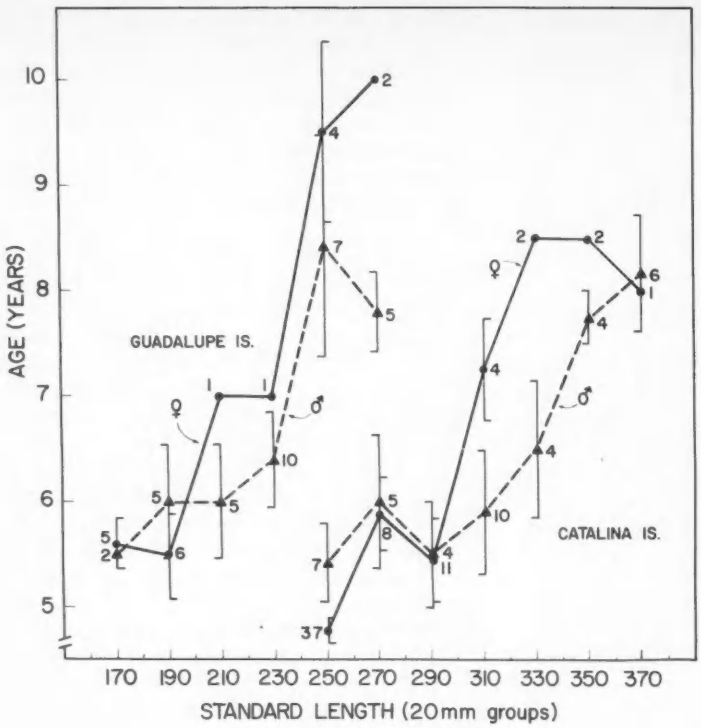

FIGURE 16.—Mean ages for successive 20 mm standard length groupings of male and female *Pimelometopon pulchrum*. Sample sizes and standard errors are shown as in Figure 15.

The best picture, then, that can be drawn from the present information is that rapidly growing individuals may transform sooner than other fishes of the same age. The bulk of the population, growing at the average rate, eventually reaches a "critical" size where most of them change sex. Fishes that grow slowly may not change sex at all.

The Breeding Season, Multiple Spawning, and Fecundity

Breder and Rosen (1966) have summarized the information available on the spawning seasons of labrids. In temperate species, most activity occurs over a period of approximately 3 mo, most commonly in April, May, and June. The Catalina population of *P. pulchrum* is exceptional in this case, since spawning occurs from August to October. The two other wrasses commonly found at Catalina Island also spawn later in the year than other labrids. *Oxyjulis californica* spawns from May until October (Bolin 1930), and *Halichoeres semicinctus* probably spawns in late June, July, and August (D. R. Diener, pers. commun.). The relatively late spawning seasons of these species may be caused by upwelling along the southern California coast which usually persists well into June or July, resulting in a delay of inshore water warming until that time (Quast 1968).

Multiple spawning has not often been considered in studies of labrid breeding seasons. Roede (1972) stated that labrids have "continuous, successive spawning cycles," and based this view upon the presence of many vitellogenic oocyte stages in mature ovaries of the seven species she investigated. She contended there is no resting stage of the ovary, but a series of year-round spawnings. At all times of the year she was able to find ovaries with several stages of developing oocytes as well as the stage 2 recruitment stock. This clearly is not the case in *P. pulchrum*, where the winter-resting ovary contains virtually no signs of vitellogenesis. Active ovaries of the California sheephead strongly resemble those pictured by Roede (1972, plates II and III) for *Halichoeres* and *Hemipteronotus*. The successive spawnings within a restricted season indicated for *P. pulchrum* may then be a curtailed version of a

year-round condition in its presumably tropical ancestor, representing an adaptation to the fluctuations of food availability characteristic of temperate regions.

The size-specific increases in fecundity seen in Catalina *P. pulchrum* are, of course, common in most long-lived fishes. Many of the Guadalupe females were not sexually active when the sample was taken and no fecundity data are available. However, it can be predicted that the average fecundity of Guadalupe Island individuals will increase much more slowly with age than that of individuals from Catalina, due to the low growth rate of the Guadalupe individuals discussed in an earlier section. If the active ovary weight increases with size in a fashion similar to that seen at Catalina (Figure 13), the average ovary weight for a 4-yr-old fish at Guadalupe would be approximately 8 g. Age class 4 California sheephead at Catalina had ovaries with an average weight of 13.13 g. The difference increases with age. Six- and eight-year-old individuals at Guadalupe should have ovaries weighing 9 and 15 g respectively. Weights for the same ages at Catalina were 23.1 g and 53.5 g.

In the Catalina population, there may be an abrupt increase in the fecundity of fishes remaining female after age seven; this is the age where most sexual transformations occur (compare Figures 9 and 14). If such an increase does exist, it may be an indication of compensation by those remaining females for the relative gain in age-specific reproductive potential experienced by individuals that do change sex. A more complete discussion of relative male and female age-specific fecundities can be found elsewhere (Warner in press).

The Relationship of Color and Sex

Pimelometopon pulchrum appears to follow the general labrid coloration pattern quite closely, with a preponderance of females and immatures in the initial uniform color phase, and the terminal bicolored phase containing only males. Thus the designation of the uniform phase as the "female" coloration and the bicolored phase as the "male" coloration (Jordan and Evermann 1898; Fitch and Lavenberg 1971; Miller and Lea 1972) is more or less correct, especially when immatures are included under the uniform designation (Barnhart 1936; Roedel 1948). Dichromatism, however, is not necessarily an indication of sexual dimorphism in the Labridae, and extensive sampling is usually needed before the relationship between sex and coloration can be accurately described.

Many labrid species exhibit a number of color phases, and these have often been attributed to sexual dimorphism or to differences between immatures and adults. Roede (1972) has reviewed a number of cases where such an interpretation was incorrect, being based on casual observation or small samples. Apparently there is no strict distribution of sex with color in the Labridae and the only generalization possible is that females tend to strongly predominate in the "first adult" (Roede 1972) colors, and the terminal-phase coloration is made up almost exclusively of males.

In most species investigated, males make up 10 to 35% of the first adult-colored individuals (Roede 1972). In *Gomphosus varius* (Strasburg and Hiatt 1957), *Halichoeres maculipinna*, *H. garnoti*, and *Hemipteronotus martinicensis* (Roede 1972), no males are found in the initial color phase. In contrast, Söljan (1930a, b) found that 48% of the *Symphodus* (*Crenilabrus*) *ocellatus* examined in the first adult phase were males.

The terminal-phase coloration appears to be much more closely restricted as to sex. Of 14 labrid species exhibiting color phases mentioned by Roede (1972), the terminal phase consisted exclusively of males in all but two (*Halichoeres garnoti* and *H. bivittatus*). When other coloration classes are described, intermediate between the initial and terminal phases, the proportions of males and females in them are also intermediate. Roede (1972) notes that where color changes are more gradual, as in *H. garnoti* and *H. bivittatus*, the relationship between size and sex is the least exact.

Sex Ratio and an Estimate of Survival

Roede (1972) believed that her collections were true random samples of populations and was able to estimate the sex ratio in the seven labrid species she investigated. There were two to four times as many females as males in all but one species (*Hemipteronotus splendens*), which had an equal sex ratio.

The samples of *P. pulchrum* were not considered random and direct sex ratio estimates could not be made. Field transects at Catalina and Guadalupe islands yielded a ratio of about 5.5 uniformly colored individuals to every bicolored male. To estimate the sex ratios of mature individuals, the

proportion of immatures and males in the uniform group must be known, and this requires some knowledge of mortality rates.

A rough estimate of mortality can be made from the transect data and the known color composition of each age. The yearly survival rate is calculated using a modification of a simple fisheries estimate (Ricker 1958). The rate is assumed to be constant, and can be estimated as:

$$\hat{s} = \frac{N_{t+1}}{N_t}$$

where N is the number of individuals in a particular age class in a sample. Where a large number of age classes are available, one can weight the classes according to their abundance and separate two or more ages from the numerator and denominator, giving, for example:

$$\hat{s}^2 = \frac{N_3 + N_4 + \ldots + N_r}{N_1 + N_2 + \ldots + N_{r-2}}$$

For the Catalina population of *P. pulchrum*, the formula used was:

$$\hat{s}^6 = \frac{N_8 + N_9 + \ldots + N_{13}}{N_2 + N_3 + \ldots + N_7}$$

In this first approximation we assume that bicolored fishes are all 8 or more years old, and younger fish (ages 2 through 7) are uniform. The decision to use age 7 as the dividing point comes from Figure 9, where between ages 7 and 8 the proportion of females drops to a low level and the males become predominant.

From Catalina transect data, $\hat{s}$ is estimated by:

$$\hat{s}^6 = \frac{33}{183} \text{ and } \hat{s} = 0.735.$$

The transect ratio can then be adjusted to compensate for bicolored individuals younger than age 8 and uniform individuals older than age 7 by using proportions derived from Table 4, and each age's contribution to the numerator or denominator can be weighted according to the first estimate of survival derived above. The new estimate of survival from the adjusted transect ratio is not very different from the original, $\hat{s} = 0.71$.

A similar estimate for the Guadalupe Island population, assuming in this case that the uniform individuals are ages 2 through 7 (see Figure 9) and adjusting as before, is $\hat{s} = 0.69$.

Mature sex ratios can now be estimated. Using 0.7 as the yearly survival rate, about 36% of the uniform individuals seen at Catalina should be mature, and approximately 5% of those individuals would be male. The ratio of mature males to mature females from field transects would then be derived as:

$$\frac{33 + (183 \times 0.36 \times 0.05)}{183 \times 0.36 \times 0.95} = \frac{36}{63} = 0.57$$

or about two females for every mature male.

For Guadalupe, about a third (34%) of the uniform individuals should be mature, and 90% of these would be female. The sex ratio at Guadalupe would then best estimated as:

$$\frac{64 + (343 \times 0.34 \times 0.1)}{343 \times 0.34 \times 0.9} = \frac{76}{105} = 0.72$$

or approximately three females for every two males.

An artifact of protogynous hermaphroditism is the concentration of females in the younger ages. Thus, the observed sex ratio depends on when the animals change sex, and upon the mortality occurring from year to year. Mortality causes sex ratios to be biased towards females and these become even more biased the greater the average age of transformation is in the population. This effect can be seen by comparing the estimated sex ratio of the Guadalupe population (0.72), where most females change sex within 3 yr after maturity, with that of Catalina (0.57), where transformation is relatively delayed.

The deviations of sex ratio from unity seen here should not be taken as contradictions of the theories put forth on the adaptiveness of the 1:1 ratio (Fisher 1930; Bodmer and Edwards 1960; Kalmus and Smith 1960), as these were developed for nonhermaphroditic species, and sought to equalize the lifetime reproductive potentials for males and females. In sequential hermaphrodites, the same individual functions as both male and female at sometime in its life, and the question becomes one of changing sex at the proper time to maximize the individual's reproductive potential (Warner in press).

SUMMARY

Year-round sampling of a population of the California sheephead, *Pimelometopon pulchrum*, was carried out at Catalina Island, Calif., and comparative material was collected from a population at Guadalupe Island, Mexico.

Age determinations indicate individuals in the Guadalupe population are dwarfed relative to

those at Catalina. The growth rate is lower for Guadalupe fishes and in both populations there may be a slowing of growth at the onset of maturity, as well as an increase in the growth rate after sexual transformation.

Pimelometopon pulchrum is a protogynous hermaphrodite. During the sex change from female to male, the ovary degenerates and spermatogenic crypts dominate the gonad. The basic structure of the gonad remains ovarian however, with lamellae protruding into a central lumen. Sperm transport is through a series of ducts on the periphery of the gonad and oviduct.

Catalina California sheephead attain sexual maturity at age 4, at a standard length of about 200 mm. Most function as females for 4 yr and then change sex, at a length of about 310 mm. Some individuals may transform earlier or later, or not at all. The Guadalupe population also matures at age 4, at a length of about 140 mm. But transformation occurs at an earlier age, with most individuals becoming males by age 7. Peak transformation activity occurs in fishes between 190 and 230 mm SL at Guadalupe.

Gonad development states and gonad indices of Catalina California sheephead suggest that spawning occurs in July, August, and September and that sexual transformation occurs in the winter months between breeding seasons.

Spawning probably takes place a number of times in a single breeding season, which complicates the determination of the actual number of eggs produced by a female each year. Ovary weight, however, can give a good indication of relative age and size-specific fecundities, since egg density does not appear to vary with fish length. The ovary weight of *P. pulchrum* increases exponentially with length and linearly with the age of the individual in the Catalina population.

At Guadalupe, the average fecundity probably increases more slowly with age when compared to Catalina, due to the low average rate of growth.

Pimelometopon pulchrum has three color phases. Juvenile coloration occurs in individuals usually less than a year old and smaller than 100 mm in length, and never in sexually mature individuals.

The uniform coloration is found in immatures and mature females. Melanization may obscure the ground coloration, but it appears that about 5% of the mature uniform individuals were males at Catalina, and 12% at Guadalupe.

Bicolored fishes are exclusively males or late transitionals and usually have a nuchal hump and filamentous extensions of the median fins.

Field observations indicate that there are about 5.5 uniformly colored individuals to every bicolored male at both Catalina and Guadalupe.

Individual size appears to have a greater effect on the sex change than does age, and rapidly growing fishes may change sex sooner than slow growing individuals of the same age, which may not change sex at all.

With the assumption of constant, age-independent mortality, the annual survival rate at both Catalina and Guadalupe was estimated as about 0.7, as judged from the field transect data.

The mature sex ratio at Catalina was approximately two females for every male. At Guadalupe the ratio was closer to three females for every two males, due in part to the earlier sexual transformation seen there.

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AN INVERSE CORRELATION BETWEEN MERISTIC CHARACTERS AND FOOD SUPPLY IN MID-WATER FISHES: EVIDENCE AND POSSIBLE EXPLANATIONS

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ABSTRACT

In five species of mid-water fishes, *Chauliodus sloani*, *Diplophos taenia*, *Pollichthys mauli*, *Vinciguerria lucetia*, and *V. nimbaria*, the central values of meristic counts (anal fin rays, vertebrae, longitudinal photophore rows) and three measures of biological productivity (phosphate-phosphorus concentration, net primary production, zooplankton standing stocks) are correlated negatively. For the species and areas studied the meristic variation observed cannot be related to temperature, salinity, dissolved oxygen, or any other physical or chemical factor known to affect meristic variation in fishes. It is hypothesized that this relationship between meristic counts and measures of food availability involves differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences in turn reflect adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

Meristic characters have been widely used in studies of fish populations and species. Unlike body proportions or coloration, meristic characters are fixed usually at or before metamorphosis and remain constant throughout the life of an individual. Variation in meristic characters stems from both genetic variation between populations and species, and from environmental variation, which, within genetically controlled limits, can directly affect the number of parts formed in developing embryos and larvae. Recent reviews of factors known to affect meristic characters in fishes include Barlow (1961), Blaxter (1969), Garside (1966), and Fowler (1970).

An inverse relationship between vertebral and/or other meristic counts and water temperature at the time of early development has been demonstrated in numerous studies (see above review articles). Experimental studies have shown that in many cases the effect of temperature upon meristic characters occurs within a restricted period of time, the so-called sensitive period, and that variations in temperature before and after this period have no effect (Hempel and Blaxter 1961). The sensitive period may vary with different structures with the result that the timing, magnitude, and in some cases the direction of response of different structures to temperature variation differs among different species (Fowler 1970).

Hubbs (1926), Barlow (1961), and others, have suggested that the relationship between meristic counts and temperature involves differential effects of temperature on rate of growth versus rate of differentiation, with the result that accelerated growth is associated with a shortening of the sensitive period, resulting in the laying down of fewer parts. The conclusion is that conditions retarding growth rates are associated with elevated meristic counts, conditions accelerating growth rates are associated with lowered meristic counts. This explanation has been extended to factors other than temperature known to affect meristic characters in fishes: dissolved oxygen concentration (Alderdice et al. 1958), salinity (Forrester and Alderdice 1966; Blackburn 1967), carbon dioxide concentration, light intensity, exposure to X-rays, etc. (see Fowler 1970).

In 1972, we reported a significant negative correlation between certain meristic counts in *Diplophos taenia* and three measures of food supply: net primary production, phosphate-phosphorus concentration, and zooplankton standing stocks (Johnson and Barnett 1972). To our knowledge, this was the first suggestion of a

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possible relationship between meristic counts and measures of food supply. We did not offer any explanation for this relationship in the earlier report. In the present paper we extend our information on *D. taenia* to the Atlantic Ocean, present corroborative evidence for the relationship between meristic counts and food supply based on four other species of mid-water fishes, and attempt to show that the relationship for the species and areas studied is with food supply and not temperature, salinity, or dissolved oxygen. We hypothesize that this relationship between meristic counts and food supply reflects differences in egg size, fecundity, size at hatching, and size at comparable stages of larval development between populations in different areas, and that these differences represent adaptations to low food densities in areas of low productivity and higher predator densities in areas of higher productivity.

METHODS

Collection and Analysis of Data

Methods of taking counts follow those of Grey (1964), Morrow (1964), and Johnson (1970). Photophore rows in a generalized stomiatoid fish are illustrated in Morrow (1964: Figure 73), but our nomenclature for segments of photophore rows follows that of Johnson (1970). All vertebral centra were counted including the compound element supporting the parhypural and hypurals (Weitzman 1967). Standard statistical texts have been used as reference material (especially Tate and Clelland 1957; Sokal and Rohlf 1969). Agreement between sets of ranks is assessed via the tau coefficient of correlation or Kendall's coefficient of concordance, W (see Tate and Clelland 1957).

Localities Studied

We have studied specimens from eight areas (Figure 1): 1) the eastern tropical Pacific (ETP) off Mexico; 2) the central North Pacific (CNP) off the Hawaiian Islands; 3) the central equatorial Pacific (CEP) at long. 145° to 150°W; 4) the western equatorial Pacific (WEP) around long. 170°E; 5) the Philippine Sea (PS); 6) the South China Sea (SCS); 7) the Gulf of Guinea (GG); and 8) the central North Atlantic (CNA) including the Sargasso Sea. All of these areas are tropical oceanic habitats and represent a wide range of physical and biological features.

Measures of Biological Productivity

The measures used to assess relative richness of food supply are phosphate-phosphorus concentration, net primary production, and zooplankton standing stocks. These three variables are highly intercorrelated (Cushing 1971). These measures were chosen because there are published attempts at contouring values of these variables on an oceanwide basis and because values for them are commonly reported in more regionally oriented studies.

Despite many problems in both sampling and interpretation associated with attempts to contour values of biological variables on an oceanwide basis and to integrate values based on a limited number of measurements over a full year, we were forced to accept such attempts as the principal basis for ranking our eight study areas with respect to the three measures of food supply. Where possible we relied on synoptic studies presenting contours on an oceanwide basis: net primary production (as mg-C/m^2 per day, Koblentz-Mishke et al. 1970; as g-C/m^2 per year, Ebeling 1962 based on Fleming and Laevastu 1956), zooplankton concentration (as parts/10^6 by volume in the upper 150 m of the Pacific Ocean, Reid 1962), and phosphate-phosphorus concentration (as μg-at/liter contoured at 100 m in the Pacific Ocean, Reid 1962). Where these studies did not cover several of our study areas, we used regional studies (SCS: Angot, Steemann Nielsen in Wyrtki 1961; Sorokin 1973; GG: Raymont 1963, Corcoran and Mahnken 1969, Kinzer 1969, Zeitschel 1969, Riley 1972; CNA: Menzel and Ryther 1961, Raymont 1963, Corcoran and Mahnken 1969, Zeitschel 1969, Riley 1972).

We compared the contours or values for each of the three measures of productivity over all eight study areas and then ranked the eight areas with respect to each other for each measure (Table 1). As expected (Cushing 1971), the ranks for the three measures over the eight areas are highly concordant ($W_{3,8} = 0.85$, $P < 0.01$, concordance coefficient corrected for ties, see Tate and Clelland 1957). This highly significant concordance increases our confidence in this approach to ranking the eight areas with respect to productivity and allows summation of the ranks of the three measures of food supply over each area, yielding a rank-sum. We then ranked this rank-sum and obtained the following rank-index order of productivity, from highest to lowest: 1) eastern

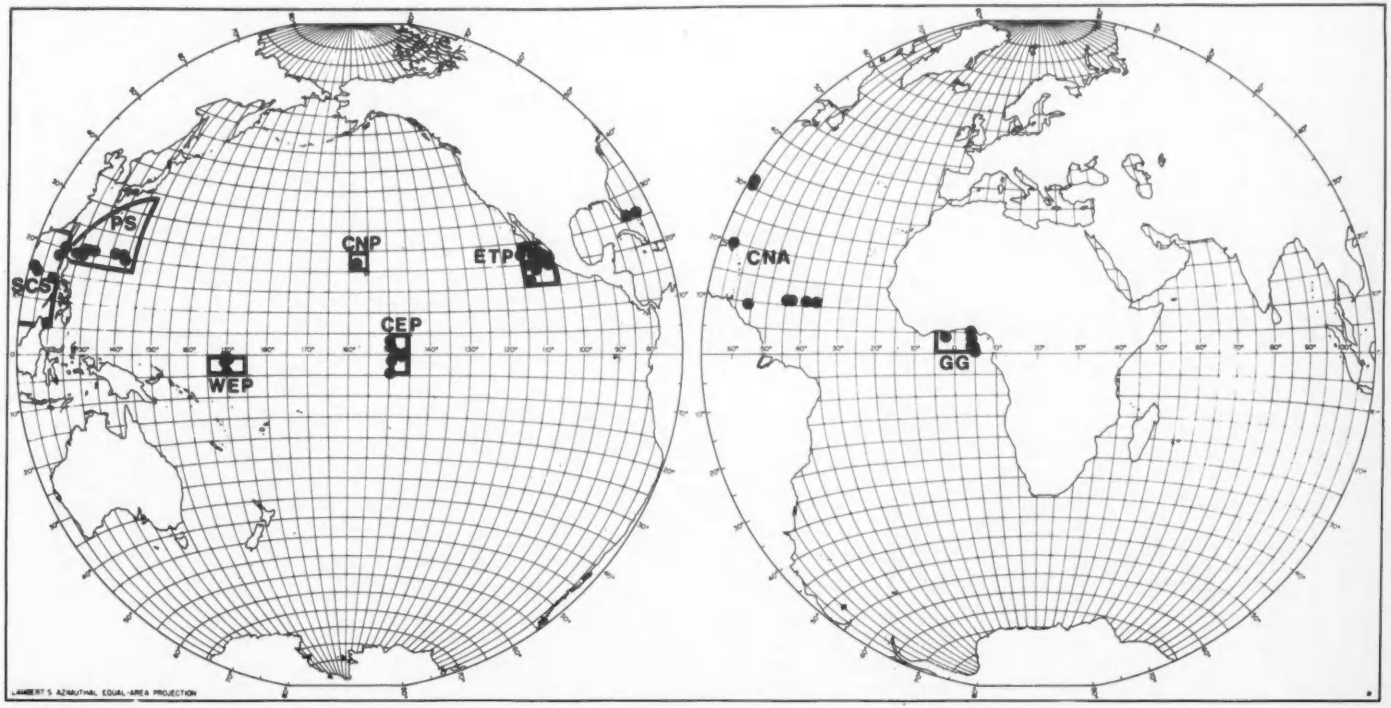

FIGURE 1.–Study areas: ETP = eastern tropical Pacific; CEP = central equatorial Pacific; CNP = central North Pacific; WEP = western equatorial Pacific; PS = Philippine Sea; SCS = South China Sea; GG = Gulf of Guinea; CNA = central North Atlantic. Localities for *Diplophos taenia* indicated by closed circles. Localities for other species were within boundaries of study areas as indicated except that all specimens of *Vinciguerria nimbaria* from the central North Atlantic were from the Ocean Acre area near lat. 32° to 33°N, long. 64°W.

TABLE 1.–Computation of rank-sum index of productivity. This table was produced by reproducing the contours or values presented by each of the authors cited in the text for each of the three measures of productivity–net primary production (NET), zooplankton concentration (ZOO), and phosphate phosphorus concentration (PO_4-P)–within the geographic limits of each of the eight areas and then ranking the eight areas with respect to one another for each measure.

Area	NET rank	ZOO rank	PO_4-P rank	Sum of ranks	Rank-sum
ETP	1	1	1	3	1
GG	2.5	3.5	2	8	2
SCS	2.5	[1]3.5	4.5	10.5	3
CEP	4	5	3	12	4
WEP	7	2	4.5	13.5	5
PS	5	6	7.5	18.5	6
CNA	6	7	6	19	7
CNP	8	8	7.5	23.5	8

$W_{3,8} = 0.85$, $P < 0.01$

[1]Data from Brinton (pers. commun.)

tropical Pacific, 2) Gulf of Guinea, 3) South China Sea, 4) central equatorial Pacific, 5) western equatorial Pacific, 6) Philippine Sea, 7) central North Atlantic, and 8) central North Pacific. In establishing the relationship between meristic counts and productivity we have compared central values of meristic counts with this rank-index value for productivity.

RESULTS

Diplophos taenia Günther

Diplophos taenia, a circumtropical mesopelagic gonostomatid, is the only species included in this study to occur in all eight study areas. Results for counts of anal fin rays, LLP photophores, and IPVALA photophores are illustrated in Figure 2. In nearly all cases counts are highest in areas of lowest productivity, lowest in areas of highest productivity, and intermediate in areas of intermediate productivity. Agreement between mean values for photophore row segments in terms of rank order by area, e.g. all four segments in the IC row, is highly significant ($W_{4,8} = 0.81$, $P < 0.01$, Table 2), as is the agreement between mean values for anal fin rays, LLP photophores, and IPVALA photophores ($W_{3,8} = 0.94$, $P < 0.01$, Table 3). This concordance allows computation of a rank-sum index for mean values of meristic counts (Table 3).

There exists no significant correlation between the observed meristic variation and temperature over the six Pacific areas ($tau_6 = 0.13$, $P > 0.20$, Table 4). Temperature data was taken from a chart of temperature at 100 m in the Pacific Ocean

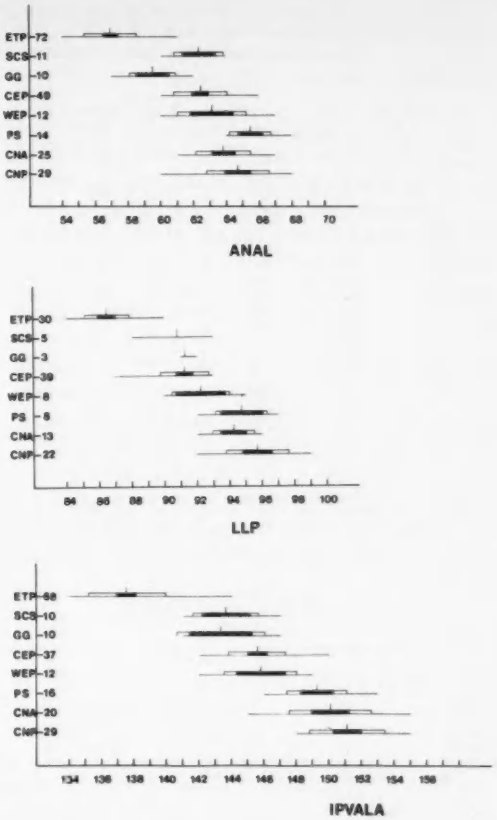

FIGURE 2.–*Diplophos taenia*. Comparison of mean (vertical line), 95% confidence limits for the mean (closed bar), one standard deviation on either side of the mean (open bar plus closed bar), and range (horizontal line) for anal fin rays (top), LLP photophores (middle), and IPVALA photophores (bottom) for specimens from eight study areas (Figure 1). Numbers on ordinate are number of specimens examined.

TABLE 2.–Agreement between segments of IC row of photophores in *Diplophos taenia*. Values are given as mean)rank. Number of specimens (n) is given for counts of IP and represent the minimum number of specimens counted for each character for each area.

Area	n	IP	PV	VAV	AC	Sum of ranks
ETP	74	15.7)8	24.9)8	15.1)8	42.0)8	32
GG	10	16.6)6	27.1)2.5	15.9)5	42.9)7	20.5
SCS	10	16.4)7	25.6)7	16.0)4	44.7)6	24
CEP	50	16.9)5	26.2)6	15.8)6	45.18)4	21
WEP	12	17.0)4	26.4)5	15.7)7	45.17)5	21
PS	18	17.1)3	26.9)4	16.3)2	46.67)3	12
CNA	25	17.4)1	27.5)1	16.2)3	46.72)2	7
CNP	29	17.3)2	27.1)2.5	16.6)1	47.5)1	6.5

$W_{4,8} = 0.812$, $P < 0.01$

TABLE 3.—*Diplophos taenia*, computation of rank-sum index of meristic counts and comparison with rank-sum index of productivity (from Table 1). Values are given as mean (number of specimens).

Area	Anal fin Mean	Rank	LLP Mean	Rank	IPVALA Mean	Rank	Sum of ranks	Rank-sum	Productivity rank-sum
ETP	57.0 (72)	8	86.5 (30)	8	137.5 (68)	8	24	8	1
GG	59.5 (10)	7	91.3 (5)	5	143.3 (10)	7	19	6.5	2
SCS	62.3 (11)	6	90.8 (3)	7	143.6 (10)	6	19	6.5	3
CEP	62.4 (49)	5	91.2 (39)	6	145.54 (37)	5	16	5	4
WEP	63.2 (12)	4	92.2 (8)	4	145.75 (12)	4	12	4	5
PS	65.4 (14)	1	94.8 (8)	2	149.2 (16)	3	6	2	6
CNA	63.8 (25)	3	94.2 (13)	3	150.2 (20)	2	8	3	7
CNP	64.7 (29)	2	95.7 (22)	1	151.7 (29)	1	4	1	8

$W_{3,8} = 0.942$, $P < 0.01$ $\quad$ $Tau_8 = -0.893$, $P < 0.01$

TABLE 4.—*Diplophos taenia*. Comparison of rank-sum index of meristic counts (from Table 3) with temperature at 100 m ranked over the six Pacific areas. Temperature data taken from Brinton (1962).

Area	Rank: Counts	Rank: Temperature
CNP	1	5
PS	2	3.5
WEP	3	1
CEP	4	2
SCS	5	3.5
ETP	6	6

$Tau_6 = +0.13$, $P > 0.20$

given by Brinton (1962). The 100-m depth was chosen arbitrarily, but the conclusion holds if surface temperatures, whether summer or winter, are chosen. Meristic counts for *D. taenia* are lowest in specimens from the eastern tropical Pacific where temperature values are also the lowest. This is exactly opposite to the result expected if temperature were involved in determining the meristic variation observed over the six areas. In fact the data show no relationship between meristic counts and temperature for these areas. Values of salinity in the open ocean are far too conservative to be involved in determining the observed variation (Hubbs 1925; Sverdrup et al. 1942; Barlow 1961; Blackburn 1967). Although the eastern tropical Pacific is well known for a marked oxygen minimum layer (Brandhorst 1959), and oxygen concentration variation may affect the development of meristic characters (Alderdice et al. 1958; Garside 1959, 1966), in all eight areas oxygen is essentially saturated in the wind-mixed surface layer where the larvae and probably the eggs of *D. taenia* occur. The low counts (relative to other areas) of specimens of *D. taenia* from the eastern tropical Pacific run counter to what might be expected if dissolved oxygen concentrations were involved in determining the observed meristic variation.

The rank-sum indices of meristic counts and productivity are significantly and negatively correlated ($tau_8 = -0.893$, $P < 0.01$, Table 3).

Pollichthys mauli (Poll)

Pollichthys mauli ranges from the western North Atlantic to the Philippine Sea. We have examined specimens of this species from the Gulf of Guinea, and the Philippine and South China seas. Results for IPVALA photophore counts (Table 5) parallel the results for *Diplophos taenia;* the counts from Philippine Sea specimens are significantly higher than counts from specimens from the South China Sea and Gulf of Guinea.

TABLE 5.—*Pollichthys mauli*, IPVALA photophores.

Area	68	69	70	71	72	73	74	75	76	77	78	*n*	Mean ± 95% limits
GG	1	7	5	6	1	4	–	–	–	–	–	24	70.46 ± 0.635
SCS	–	–	1	7	2	1	–	–	–	–	–	11	71.27 ± 0.528
PS	–	–	–	–	–	1	1	3	2	1	2	10	75.70 ± 1.170

Vinciguerria lucetia Garman

Vinciguerria lucetia is endemic to the eastern Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The work of Ahlstrom and Counts (1958) has made the early life history of *V. lucetia* the best known of any of the species included in this report. We have not examined any specimens of *V. lucetia* in connection with this work, but the following results of the study of this species by Ahlstrom and Counts (1958) seem to be particularly relevant to this paper: 1) In *V. lucetia* the total number of myotomes is formed in late-stage eggs, prior to hatching. 2) Metamorphosis in *V. lucetia* is marked by a period of rapid change in body proportions without a marked change in standard length. The completion of metamorphosis is signaled by the complete development of all photophores, including the late-forming photophores of the posterior VAV and mid-AC segments. 3) Metamorphosis occurs at a smaller size south of lat. 25°N than north of lat. 27.5°N, with meta-

morphosis at an intermediate size in specimens from lat. 25° to 27.5°N. Mean values of vertebral and IPVALA counts are lowest in specimens taken from areas where metamorphosis occurs at a smaller size. A delay in vertebral ossification is found in specimens from areas where metamorphosis occurs at a larger size. 4) Ahlstrom and Counts (1958) report a north to south cline in mean values for IPVALA photophore counts and relate this to temperature. An east to west cline is also suggested by their data (Figure 3), with mean IPVALA counts lowest near the American continent and increasing with distance offshore. Values for productivity measures in the eastern tropical Pacific tend to fall off with increasing distance from land (Reid 1962; Koblentz-Mishke et al. 1970). If variation in photophore numbers in *V. lucetia* is related to variation in productivity, we would expect mean IPVALA counts at a given latitude to be lower near the continent and higher with increasing distance from land. Data from Ahlstrom and Counts (1958) confirm this expectation (Figure 3) for all but two latitudinal transects. Along these two transects, one just to the north of the equator, the second centered at about lat. 12°N, mean values obtained for IPVALA counts do not change or actually decrease to the westward, an apparent contradiction of our hypothesis. However, these two zonal transects fall along zonal areas of high or elevated productivity far to the westward of the American continent, and this is true for net primary production, zooplankton standing stocks, or, as illustrated (Figure 3), phosphate-phosphorus concentration. Williams (1972) relates these zonal belts of elevated productivity to the divergence systems at the equator and at the North Equatorial Countercurrent-North Equatorial Current boundary. Williams (1972) states that the zonal band at lat. 10° to 12°N is best shown by data for zooplankton stocks, but we note that this band is quite apparent for phosphate-phosphorus concentration (Reid 1962). Thus the apparently discrepant values of mean IPVALA counts from specimens of *V. lucetia* taken along these two zonal transects in fact tend to further corroborate the hypothesized inverse relationship between meristic counts and productivity.

Vinciguerria nimbaria (Jordan and Williams)

Vinciguerria nimbaria is nearly circumtropical in distribution but does not occur in the Medi-

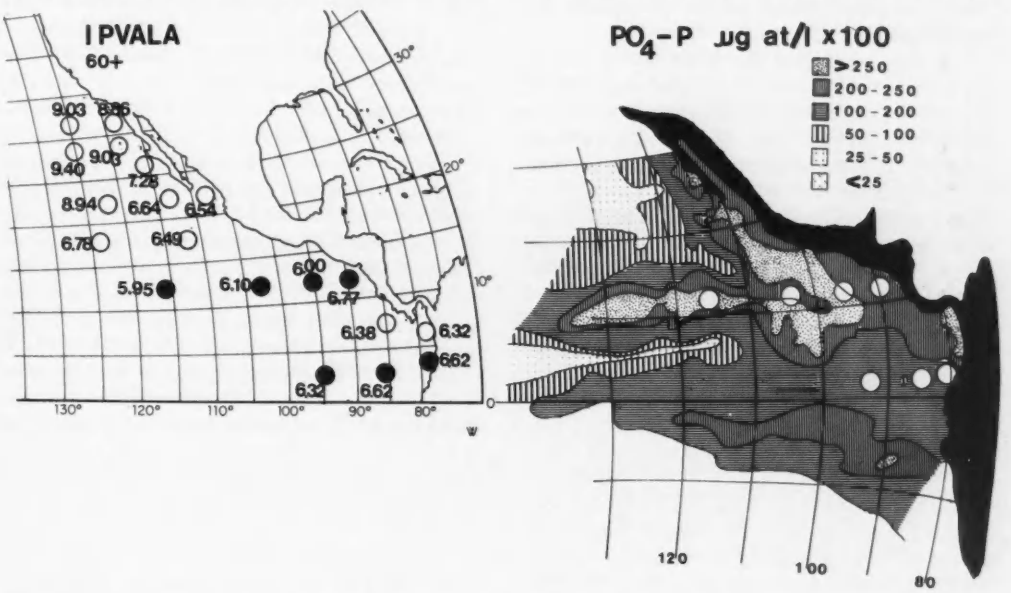

FIGURE 3.—*Vinciguerria lucetia*. Left: IPVALA photophores; values given are means based on five or more specimens taken at each locality (see text for additional explanation, data from Ahlstrom and Counts 1958). Right: phosphate phosphorus data simplified from Reid (1962).

terranean Sea nor in the eastern tropical Pacific (Ahlstrom and Counts 1958; Craddock and Mead 1970; Gorbunova 1972). The development of larvae of *V. nimbaria* is apparently quite similar to the development of larvae of *V. lucetia* (Ahlstrom and Counts 1958; Silas and George 1971). We have examined specimens of *V. nimbaria* from all of our study areas except the eastern tropical Pacific (where *V.nimbaria* is replaced by *V. lucetia*) and the western equatorial Pacific (no material available).

Counts of IPVALA photophores for specimens of *V. nimbaria* are given in Table 6. Mean values for specimens from the South China Sea, central equatorial Pacific, Philippine Sea, central North Atlantic, and central North Pacific agree in perfect rank-order with the rank-sum index of meristic counts for specimens of *Diplophos taenia* from these five areas (Table 3). The mean value of counts of IPVALA photophores of Gulf of Guinea specimens does not fit this trend, it is too high. All of our material of *V. nimbaria* from the Gulf of Guinea came from a single collection at the University of Miami (UMML 21902, lat. 0°54′ to 1°05′N, long. 4°53′ to 4°51′E, 23-24 May 1965). We have neither additional material of nor information on *V. nimbaria* from the Gulf of Guinea, and, for the present, we are unable to explain these anomalous results.

The values obtained for specimens of *V. nimbaria* from other study areas support our hypothesis of an inverse relationship between meristic counts and productivity. This is true for both IPVALA photophore (Table 6) and vertebral (Table 7) counts.

Counts for Arabian Sea (AS, Table 6) specimens of *V. nimbaria* are taken from Silas and George (1971). They studied specimens taken off the Malabar Coast of India and found larvae of *V. nimbaria* to be most abundant along the edge of the continental shelf from Mangalore to south of Cochin. Cushing (1971) discusses the strong upwelling system occurring along this coast during the period of the Northeast Monsoon, and notes that high values of productivity occur in this area over at least half of the year and are associated with the upwelling system. Silas and George (1971) found *V. nimbaria* larvae to be most abundant during the upwelling season. Values for productivity measures in this area given by Cushing (1971) approach values for the eastern tropical Pacific, are certainly larger than values for the Philippine Sea, central North Atlantic, and central North Pacific, and probably significantly larger than values for the central equatorial Pacific and South China Sea. We therefore expected values for meristic counts of specimens of *V. nimbaria* from off the Mangalore Coast to be the lowest of any of these six areas. They are (Table 6).

TABLE 7.—*Vinciguerria nimbaria*, vertebrae.

Area	39	40	41	42	*n*	Mean ± 95% limits
SCS	6	5	–	–	11	39.45 ± 0.351
CEP	1	23	7	–	31	40.19 ± 0.175
PS	–	3	12	8	23	41.22 ± 0.290
CNP	–	–	6	21	27	41.78 ± 0.168

Chauliodus sloani Bloch and Schneider

Chauliodus sloani occurs in tropical and temperate waters from the North Atlantic to the eastern Pacific, although throughout large oceanic areas it is replaced by other species of *Chauliodus*. The remaining six species of *Chauliodus*, including the recently described *C. vasnetzovi* Novikova, are limited to smaller areas, each entirely within one ocean basin (Morrow 1961; Gibbs and Hurwitz 1967; Novikova 1972).

We have examined specimens of *C. sloani* only from our Philippine Sea and central North Pacific study areas, but data from other sources (Ege 1948; Blache 1964; Gibbs and Hurwitz 1967) have made it possible to compare our results for *C. sloani* with counts for this species from other areas, and with counts for the closely related species *C. pammelas* Alcock and *C. schmidti* Ege (Table 8). IC photophore counts of *C. sloani* from central gyral areas (CNP, CNA, PS) are higher than counts from specimens taken in the South

TABLE 6.—*Vinciguerria nimbaria*. IPVALA photophore counts. AS = study area of Silas and George (1971) along Malabar Coast of India in the Arabian Sea, data taken from their study. Counts presented as the average between right and left sizes of each specimen.

Area	64	64.5	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	73	*n*	Mean ± 95% limits
AS	2	1	1	1	2	–	1	–	1	–	–	–	–	–	–	–	–	–	–	9	65.56 ± 1.023
GG	–	–	–	–	–	–	–	–	–	–	2	2	5	2	7	1	1	–	–	20	70.43 ± 0.380
SCS	–	–	2	1	10	4	2	1	4	–	–	–	–	–	–	–	–	–	–	24	66.46 ± 0.378
CEP	–	–	–	–	2	2	1	2	14	6	4	1	–	–	–	–	–	–	–	32	67.98 ± 0.302
PS	–	–	–	–	1	2	1	4	24	26	20	37	83	36	16	4	2	1	–	257	69.60 ± 0.126
CNA	–	–	–	–	–	–	1	–	1	2	1	4	2	1	–	–	–	–	–	12	69.12 ± 0.623
CNP	–	–	–	–	–	–	–	–	–	–	–	3	18	15	5	1	1	–	–	43	70.34 ± 0.157

TABLE 8.—IC photophore variation in three species of *Chauliodus*. (NIO, northern Indian Ocean, TAA, TAB, areas of eastern tropical Atlantic discussed in text).

Species	Area	58	59	60	61	62	63	64	65	66	67	68	69	*n*	Mean ± 95% limits
C. pammelas[1]	NIO	1	4	12	4	—	—	—	—	—	—	—	—	21	59.90 ± 0.350
C. schmidti[2]	TAA	—	—	1	7	32	14	—	—	—	—	—	—	54	62.09 ± 0.186
C. schmidti[2]	TAB	—	—	—	3	16	14	7	5	—	—	—	—	45	62.89 ± 0.335
C. sloani[3]	SCS	—	—	—	—	1	16	69	91	25	2	—	—	204	64.32 ± 0.117
C. sloani	PS	—	—	—	—	—	—	—	3	2	4	4	—	13	66.69 ± 0.714
C. sloani[3]	CNA	—	—	—	—	—	—	—	—	3	6	3	1	13	67.15 ± 0.543
C. sloani	CNP	—	—	—	—	—	—	—	2	9	7	2	—	20	66.45 ± 0.386

[1]Gibbs and Hurwitz 1967.
[2]Blache 1964.
[3]Ege 1948.

China Sea. This agrees with results for other species discussed in this paper.

The only character diagnostically separating *C. schmidti* from *C. sloani* is the lower number of serial photophores in *C. schmidti* (Morrow 1961; Blache 1964). Similarly Gibbs and Hurwitz (1967) concluded that the only characters separating *C. pammelas* from *C. sloani* were lower meristic counts (IC, VAV, vertebrae) in *C. pammelas* and greater development of the gill filaments in *C. pammelas*, with filaments both longer and with a greater number of lamellae per side. Gibbs and Hurwitz (1967) noted that the greater gill filament development of *C. pammelas* is correlated with a well-marked oxygen minimum layer in the northern Indian Ocean habitat of this species. Gill filament length may vary intraspecifically in some wide-ranging mid-water fish species (Johnson 1974).

Both *C. schmidti*, inhabiting the eastern tropical Atlantic, and *C. pammelas*, inhabiting the northern Indian Ocean, are limited to areas of high biological productivity (Ryther and Menzel 1965; Gibbs and Hurwitz 1967; Cushing 1971). Both are distinguished from *C. sloani* by lower counts of serial photophores (and vertebrae in *C. pammelas*), and essentially only by these lower counts. In both cases the lower counts apparently agree with our hypothesized relationship between meristic counts and productivity. The counts for *C. schmidti* are from specimens taken in two areas: TAA, along the west African coast from lat. 03°56′ to 18°22′N, to the west and north of our Gulf of Guinea study area; and TAB, along the west African coast from lat. 01°20′ to 17°53′S, to the south of our Gulf of Guinea study area (Ege 1948; Blache 1964). The counts for *C. pammelas* are from specimens taken between lat. 08° and 14°N, long. 58° to 66°E, in the Arabian Sea (Gibbs and Hurwitz 1967).

In view of other results presented in this paper, particularly those for *Diplophos taenia*, we suggest that a reexamination of the status of both *C. pammelas* and *C. schmidti*, with additional study of meristic variation in *C. sloani* throughout the range of this species, are in order.

Results of the Antipodes Transect

An essentially experimental opportunity to test the hypothesized relationship between meristic counts and productivity was afforded by fishes taken by the Antipodes Expedition of the Scripps Institution of Oceanography in 1970. On this expedition 22 mid-water trawl collections were taken in the Philippine Sea and six mid-water trawl collections were taken in the South China Sea (Figure 4). Because of the 2,000 m or more sill depth separating these geographically contiguous areas, the upper water mass in both areas is the same and differences in physical parameters are minimal. Although the South China Sea is poorly known, there is little doubt that at least nearshore areas or areas over shelves of the South China Sea are substantially more productive than offshore areas in the Philippine Sea (Wyrtki, 1961; Sorokin 1973).

We predicted: 1) that values of meristic counts for species occurring in both the South China Sea and Philippine Sea would be lower in specimens from the South China Sea, and 2) that values of meristic counts for species occurring in the Philippine Sea would be lower in specimens taken near land and increase with increasing distance from shore.

In all four cases thus far examined (Figure 4) where differences exist in values of meristic counts from the two areas, the counts are significantly lower in specimens from the South China Sea. This supports our first prediction.

Vinciguerria nimbaria was the only species taken in sufficient abundance to allow a test of our

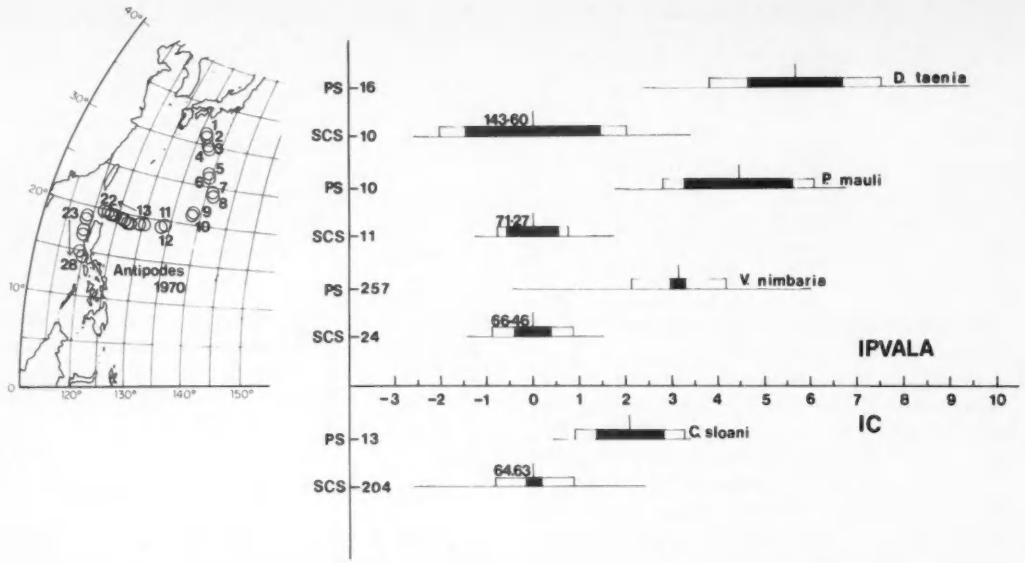

FIGURE 4.–Left: Antipodes Expedition station positions. Right: Comparison of IPVALA and IC photophore counts between specimens from South China Sea (SCS) and Philippine Sea (PS). Data presented as in Figure 2 except that mean values for South China Sea material of all four species have been set equal to zero and all other statistics are plotted as deviations from this zero point. Data for *Chauliodus sloani* from SCS are from Ege (1948); the rest is original data.

second prediction. In Table 9 mean IPVALA counts for Philippine Sea specimens of *V. nimbaria* are tested for relationship with distance of site of collection from land (Japan, Ryukyu Islands, Luzon, but not Bonin or Volcano islands). While the highest mean counts were found in specimens from the 4 stations most distant from land, the data show no relationship between mean counts and distance from land (tau_{11} = -0.273, $P > 0.20$). Mean IPVALA values for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean IPVALA values for specimens from the South China Sea.

DISCUSSION

One fact and two assumptions are prerequisite to our discussion of the possible explanations for the relationship between meristic counts and measures of food supply. The fact: in *Diplophos taenia*, *Vinciguerria lucetia*, and *V. nimbaria*, the values of the meristic characters we have studied are fixed at or before metamorphosis (Ahlstrom, pers. commun., Ahlstrom and Counts 1958, Silas and George 1971). This is probably also true for *Pollichthys mauli* and *Chauliodus sloani*. This means that any explanation involves factors operating on eggs and/or larvae. The assumptions: 1) that the meristic variation observed is not the result of selection for certain absolute values of the meristic counts, and 2) that the same basic mechanism underlies the variation in counts for all five species in the area studied (in this discussion we ignore results for specimens of *V. nimbaria* from the Gulf of Guinea).

There are four possibilities: 1) that the observed variation is ecophenotypic, i.e. nongenetic modification of the phenotype resulting from the effects of differing food availability conditions upon early growth and development of meristic characters; 2) that the observed variation is a by-product and indicative of genetic differences between populations in these eight areas, and that these differences reflect differing selective pressures resulting from differing conditions for early growth; 3) that the observed variation is a combination of ecophenotypy and genetic differences; and 4) that the real explanation is none of these, that a causal relationship between meristic characters and productivity does not exist, and that we have overlooked the real meaning of our results. We are unable to deal with the third pos-

TABLE 9.—IPVALA photophore counts of *Vinciguerria nimbaria* from the Philippine and South China seas. Antipodes station positions given in Figure 4. Distance from shore (Philippine Sea stations only) given in rank order from nearest to land to most distant offshore. R_m = rank of mean, R_d = rank of distance offshore.

Antipodes stations	65	65.5	66	66.5	67	67.5	68	68.5	69	69.5	70	70.5	71	71.5	72	72.5	*n*	Mean ± 95% limits	R_m	R_d
1, 2	–	–	–	–	–	–	2	–	1	1	3	1	1	–	1	–	10	69.80 ± 0.895	4	4
3, 4	–	–	–	–	–	–	3	4	3	2	4	3	3	–	–	–	22	69.47 ± 0.456	8	5
5, 6	–	–	–	–	–	–	2	2	2	1	12	8	1	–	–	–	28	69.84 ± 0.308	3	8
7, 8	–	–	–	–	–	–	1	–	2	4	10	3	1	–	–	1	22	69.95 ± 0.374	2	11
9, 10	–	–	–	–	–	–	–	–	–	2	3	2	3	–	–	–	10	70.30 ± 0.420	1	10
11, 12	–	–	–	–	–	–	1	1	2	–	1	1	–	–	–	–	6	69.17 ± 0.930	10	9
13, 14	–	–	–	–	–	1	1	1	2	3	4	1	–	–	–	–	13	69.31 ± 0.531	9	7
15, 16	–	–	–	–	–	–	1	–	1	–	1	2	1	–	–	–	6	69.83 ± 1.124	5	6
17, 18	–	–	–	–	1	1	5	6	2	1	6	3	1	–	–	–	26	69.06 ± 0.440	11	3
19, 20	–	–	–	–	–	–	1	4	–	3	3	1	1	1	–	–	14	69.54 ± 0.604	7	2
21, 22	–	–	1	2	–	2	7	8	5	20	36	11	4	3	1	–	100	69.59 ± 0.209	6	1
Philippine Sea, mean = 69.60 ± 0.126																		Tau_{11} = –0.273 P>0.20		
23, 24	1	1	5	1	–	1	–	–	–	–	–	–	–	–	–	–	9	66.06 ± 0.524		
25, 26	1	–	1	1	–	–	3	–	–	–	–	–	–	–	–	–	6	66.92 ± 1.345		
27, 28	–	–	4	2	2	–	1	–	–	–	–	–	–	–	–	–	9	66.56 ± 0.524		
South China Sea, mean = 66.46 ± 0.378																				

sibility and ignore the fourth possibility in our subsequent discussion.

We believe that the observed meristic variation is the result of genetic differences between populations and not the result of an ecophenotypic effect of food availability conditions on development of meristic characters. We present evidence available to support this belief, but we note that this evidence is not conclusive.

A statement of the ecophenotypic explanation is easily made. The meristic variation observed could result if the effect of low food densities upon the development of meristic characters parallels the effect of low temperature, retarding growth rates more than differentiation rates, and lengthening the period of determination of meristic characters. Because the effect of low food availability upon egg maturation appears to be a reduction of egg number and not egg size (Anokhina 1960; Blaxter 1969), any ecophenotypic effect of low food density upon meristic characters would have to operate between the onset of feeding and metamorphosis. Riley (1966) and Blaxter (1969), among others, have found for the species they have studied that the time to reach metamorphosis may be significantly increased by decreasing the density of food. Therefore an indispensable condition of the ecophenotypic explanation is that for the species studied, the final values of meristic counts are determined after the onset of feeding. If so, the meristic variation observed might result from a concordant increase in the length of the period of determination of meristic characters with a delay in time to reach metamorphosis in larvae from areas of lower productivity.

Three facts resulting from the study of the development of the eggs and larvae of *Vinciguerria lucetia* by Ahlstrom and Counts (1958) appear to support the ecophenotypic explanation: 1) Ahlstrom and Counts did find a direct relationship between size at metamorphosis (no developmental time scale is available for any of the species studied) and numbers of longitudinal photophores and vertebrae; 2) vertebral ossification and photophore formation in *V. lucetia* occur in larvae 11 mm SL or more in size, well after yolk-sac absorption and presumably after the onset of feeding; and 3) the distances between samples of *V. lucetia* utilized in construction of Figure 3 are small, much less in most cases than the distances between the eight study areas for the other species discussed in this paper. Yet the results for *V. lucetia* along the east to west transect lines apparently agree with results for the other mid-water species. We find it difficult to believe that the results for *V. lucetia* are explainable in terms of genetically distinct populations distributed along these inshore to offshore transects.

Three lines of evidence appear to contradict the ecophenotypic explanation in favor of the explanation hypothesizing that the observed meristic variation is the result of genetic differences between populations. (1) in *Vinciguerria lucetia* the total number of myomeres are formed in late stage eggs (Ahlstrom and Counts 1958). Since the number of myomeres, vertebral counts, and longitudinal photophore row counts are usually highly intercorrelated, the ecophenotypic explanation appears to be invalid in

this case. (2) The data for *Vinciguerria nimbaria* may indicate the existance of separable populations in our different study areas. This is suggested by the results for the Antipodes transect (Table 9) in which is found no clear evidence for an onshore to offshore trend toward higher IPVALA counts, despite the fact that the productivity measures are higher inshore and decrease (rapidly) to seaward (Reid 1962; Koblentz-Mishke et al. 1970). Mean values of IPVALA photophore counts for specimens from each of the 11 pairs of Philippine Sea stations are significantly higher than the mean value for South China Sea specimens. This may suggest that genetically distinct, separable populations of *V. nimbaria* are found in each area. Gill raker counts for *V. nimbaria* (Table 10) apparently support this suggestion in that counts of gill rakers are discordant with counts of IPVALA photophores (Table 6) and vertebrae (Table 7). For the four Pacific areas the counts of vertebrae and IPVALA photophores for *V. nimbaria* agree in perfect rank-order with the IPVALA photophore counts for *D. taenia* (Table 10). That this is not true for gill raker counts may indicate the existence of separable populations of *V. nimbaria* in the South China Sea, central equatorial Pacific, and the North Pacific central gyral areas (Philippine Sea, central North Pacific). (3) The ecophenotypic explanation implies that in areas of low productivity elevated meristic counts result from retardation of growth and that this retardation is the result of the average survivor being underfed compared to larvae in areas of higher productivity. As year class strength in pelagic fish populations is probably largely determined in early stages of larval life and not by the total number of eggs produced or mortality during advanced prerecruit stages (Hempel 1965), it seems likely that selection would strongly favor any mechanisms that tended to protect the larvae of mid-water fishes occurring in areas of low productivity against starvation. The possible materials on which this selection might operate and the possible consequences on meristic characters form the basis for a second explanation of the observed meristic variation, that it is the by-product of genetic differences between separable populations in areas of low and high productivity.

TABLE 10.—*Vinciguerria nimbaria*, comparison of gill raker counts with vertebral and longitudinal photophore row counts.

V. nimbaria, total gill rakers on first gill arch.

Area	17	18	19	20	21	22	23	24	25	26	*n*	Mean ± 95% limits
GG	–	–	–	–	–	–	3	6	10	1	20	24.45 ± 0.386
SCS	4	7	3	1	–	–	–	–	–	–	15	18.07 ± 0.489
CEP	–	–	–	4	13	13	1	–	–	–	31	21.35 ± 0.277
PS	–	2	26	54	31	2	–	–	–	–	115	20.04 ± 0.147
CNA	–	4	8	–	–	–	–	–	–	–	12	18.67 ± 0.313
CNP	–	–	3	6	3	–	–	–	–	–	12	20.00 ± 0.469

V. nimbaria and *Diplophos taenia*, comparison of counts, given as mean (rank.

	Vinciguerria nimbaria			*Diplophos taenia*
Area	Gill rakers	IPVALA	Vertebrae	IPVALA
SCS	18.1 (1	66.5 (1	39.4 (1	143.6 (1
CEP	21.4 (4	68.0 (2	40.2 (2	145.5 (2
PS	20.0 (2.5	69.6 (3	41.2 (3	149.2 (3
CNP	20.0 (2.5	70.3 (4	41.8 (4	151.7 (4

Hempel (1965), Blaxter (1965), and others, concerned mainly with pelagic clupeoid fishes, have developed strong evidence that under normal circumstances the main restriction on the success of a year class occurs within a short period of larval life, the critical period of Hjort (1914, 1926) and others (e.g. Marr 1956; Schumann 1965). Selection has apparently resulted in adaptive mechanisms tending to balance the two main dangers to larval survival: the danger of starvation and the danger of predation (Blaxter and Hempel 1963; Hempel 1965).

Blaxter (1965), Hunter (1972), and others, have shown that at the onset of feeding, just before or at the time of yolk-sac absorption, surprisingly small differences in size can significantly affect the probability of larval survival. Hunter (1972) has shown for northern anchovy *Engraulis mordax* Girard, larvae that slight increments in size are associated with highly increased searching abilities, highly increased success of attempted feeding acts, and vastly diminished minimum prey density requirements for survival. Blaxter (1965) discusses the significance of the greater spectrum of particle sizes available to larger larvae in terms of increased diversity of available prey organisms. Similar findings have been reported for other fish larvae (e.g. Arthur 1956; Einsele 1965). Size at hatching, at least for Atlantic herring, *Clupea harengus* Linnaeus, is a direct function of egg size; larger larvae hatch from larger eggs. Fecundity is inversely proportional to average egg size (Baxter 1959; Blaxter and Hempel 1963; Blaxter 1969).

We believe that the meristic variation between populations occurring in areas differing in productivity values is the result of adaptations involving the adjustment of egg and larval size to the productivity regime. We believe that these adaptations reflect differences between areas of low and high productivity in the relative impor-

tance of two principal dangers to larval survival: starvation versus predation.

We hypothesize that selection on mid-water fish populations inhabiting areas of low productivity has favored mechanisms tending to offset the danger of larval starvation, and that these populations will exhibit: 1) larger average egg size, 2) lower fecundity, and 3) larger average larval size at hatching and at comparable stages of development than populations living in areas of higher productivity. Advantages that might accrue to larger larvae in areas of lower productivity include increased mobility, a wider possible search volume, increased diversity of potential prey organisms, and a longer period of survivorship solely on yolk reserves.

The danger of starvation is presumably lower in areas of higher productivity but the danger of predation, resulting from presumed higher densities of potential predators on fish larvae, may be greater. Here selection may have favored increased fecundity tending to offset the danger of increased predation on larvae. We believe that in areas of higher productivity populations of mid-water fishes will exhibit: 1) smaller average egg size, 2) increased fecundity, and 3) smaller average larval size at hatching and at comparable stages of development than populations living in areas of lower productivity.

In developing this hypothesis we have largely followed Hempel's (1965) explanation for variations in egg size and fecundity between populations of herring in the eastern North Atlantic and North Sea. We note that there exists no evidence for increased predation pressure on larval populations of mid-water fishes in areas of higher productivity. It is possible to retain the main features of our hypothesis without including predation pressure by relating variation in fecundity and egg size solely to food density requirements. By definition, selection will favor maximizing reproductive output, thereby favoring fewer larger larvae in areas of low productivity where the danger of larval starvation is greater, and favoring higher fecundity (with the concomitant of smaller eggs and larvae) in areas where the danger of starvation is lessened.

There exists limited available evidence to support these predictions. Ahlstrom and Counts (1958) showed that egg size and size at hatching in *Vinciguerria lucetia* are directly related, the smallest larvae (at a defined stage of development) are found in areas where average egg diameters are least. They also showed that mean values of vertebral and IPVALA photophore counts are lowest in those areas where egg and larval size is least and where metamorphosis occurs earliest (i.e. at smallest size). Although no small larvae were available for this study, we were able to compare development in prejuvenile specimens of *V. nimbaria* from the central North Pacific with specimens from the central equatorial Pacific. In *V. nimbaria* the last four VAL photophores are late-forming, are laid down serially from anterior to posterior, usually the left member of a pair of VAL photophores develops just before the right, and the number yet to develop can be determined uniquely from the one to one correspondence with the posterior photophores in the VAV segment. In Figure 5 standard lengths of all available prejuvenile specimens of *V. nimbaria* from the central North Pacific and central equatorial Pacific are plotted against the number of VAL photophores left to appear. If this character can be used as an index to comparable stages of development, then at comparable stages of development the larvae from the area of lower productivity are the larger, as predicted.

We believe that the correlation between meristics and productivity results from a correlation between meristics and egg size, and that egg size and, hence, size at hatching are genetically determined features reflecting adaptation to productivity conditions. A number of authors have stated or suggested that such a correlation exists (Ahlstrom and Counts 1958; Lindsey 1958, 1961; Garside

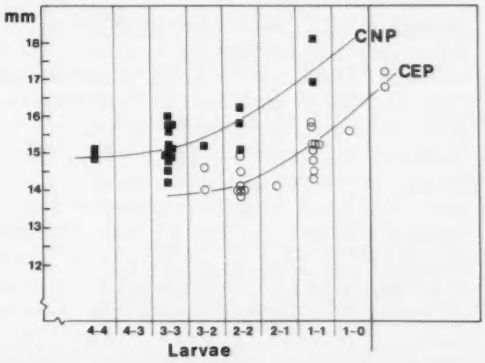

FIGURE 5.–Size of larvae of *Vinciguerria nimbaria* from the central North Pacific (CNP) and the central equatorial Pacific (CEP) at comparable stages of development. Ordinate: standard length in millimeters. Abscissa: number of VAL photophores yet to form (determined from VAV count) on each side of each specimen. Lines fitted by eye.

and Fry 1959). Lindsey and Ali (1971) have recently argued against this suggested relationship, despite the fact that their data showed a direct relationship between the number of anal fin rays and egg size in the medaka, *Oryzias latipes*. Blaxter and Hempel (1963) found no relationship between incubation time and egg size in herring, but did find a positive correlation between time to yolk sac absorption and egg size. If this correlation is true for the mid-water fishes considered in this report, if the correlation continues beyond the point of yolk sac absorption, and if the meristic characters in question are determined after hatching, it might result in a longer period of determination of these characters in larvae from larger eggs.

We lack essential developmental and ecological information to complete our hypothesis. We know little or nothing for most mid-water species about age and size at first spawning, number of spawnings per female, fecundity, seasonality of reproduction, course of larval development, or factors actually determining survivorship of larvae. The answer to the question of mechanism awaits the comparison of these population parameters between populations in areas of high and low productivity.

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MATERIAL EXAMINED

Diplophos taenia. The material examined of this species is listed in Johnson and Barnett 1972. Supplementary station list of materials examined for a study of meristic variation in *Diplophos taenia* Guenther. Ref. Ser. Scripps Inst. Oceanogr. 72-4, 1-8 (unpublished manuscript available from the Library, Scripps Institution of Oceanography, La Jolla, Calif).

Pollichthys mauli. GG: 24 (28.5-46.9), UMML 22881 (1), UMML 24132 (1), UMML 24237 (1), UMML 24266 (3), UMML 24658 (6), UMML 27884 (6), UMML 27929 (5), UMML 28159 (1). SCS: 11 (21.1-31.1); SIO 61-744 (1), SIO 69-20, (10); PS: 10 (33.8-49.9); SIO 70-308 (1), SIO 70-309 (1), SIO 70-334 (2), SIO 70-337 (2), SIO 70-340 (4).

Vinciguerria attenuata. SCS: 71 (13.0-37.8); SIO 70-341 (5), SIO 70-343 (5), SIO 70-344 (52), SIO 70-345 (5), SIO 70-346 (3), SIO 70-347 (1). PS: 71 (13.0-28.1); SIO 70-308 (12), SIO 70-309, (10), SIO 70-310 (6), SIO 70-311 (12), SIO 70-314 (11), SIO 70-318 (1), SIO 70-333 (15), SIO 70-334, (1), SIO 70-337 (2).

Vinciguerria nimbaria. GG: 20 (21.0-37.5); UMML 21902 (20). SCS: 35 (11.7-32.0); SIO 70-341 (4), SIO 70-343 (5), SIO 70-344 (10), SIO 70-345 (5), SIO 70-346 (5), SIO 70-347 (6). PS: 729 (11.6-39.9); SIO 70-306 (63), SIO 70-308 (6), SIO 70-309 (18), SIO 70-310 (23), SIO 70-311 (29), SIO 70-314 (45), SIO 70-318 (52), SIO 70-326 (7), SIO 70-327 (3), SIO 70-328 (12), SIO 70-329 (22), SIO 70-331 (2), SIO 70-332 (11), SIO 70-333 (173), SIO 70-334 (15), SIO 70-336 (6), SIO 70-337 (14), SIO 70-339 (2), SIO 70-340 (226). CEP: FMNH (Field Museum of Natural History) 77100 32 (16.9-36.0). CNA: USNM,

Ocean Acre Stations, all material from ca. lat. 32-32.5°N., long 64°W. 12(19.1-35.8); 12-17C (1), 12-18A (2), 12-18B (2), 12-28B (1), 12-34C (1), 12-35C (1), 12-62 (1), 12-80 (1), 12-81 (1), 12-86 (1). CNP: 49 (14.1-31.0); UH 69-11-5 (49).

Chauliodus sloani. PS: 14 (42.2-214.5); SIO 70-306 (3), SIO 70-311 (2), SIO 70-326 (1), SIO 70-334 (8). CNP: 20, SIO 71-301 (1), SIO 71-307 (1), SIO 71-309 (5), SIO 71-373 (1), SIO 72-11 (2), SIO 72-16 (1), SIO 72-22 (1), SIO 72-25 (2), SIO 73-142 (1), SIO 73-149 (1), SIO 73-155 (1), SIO 73-158 (2), SIO 73-159 (1).

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SPIN-LABELING TECHNIQUES FOR STUDYING MODE OF ACTION OF PETROLEUM HYDROCARBONS ON MARINE ORGANISMS

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ABSTRACT

Spin-labeling studies of membrane-contaminant interaction are being conducted by biochemists at the Northwest Fisheries Center in Seattle, Washington. The aim of these studies is to gain a better understanding of the mode of action of hydrocarbon contaminants at the molecular level. Basic spin-labeling theory together with experimental results are presented and discussed. Spin-labeling holds great promise not only for environmental studies but also for drug research, toxicology, and pharmacology as well.

The interaction between contaminants and living systems commences when contaminants combine with so-called active sites in living tissue. Active sites are varied in nature, but often they are groups of molecules assembled in a special fashion such as those which comprise membranes and associated enzymes or other biopolymers.

Although the exact nature of contaminant-host interaction may not be known in each and every case, experimental data from biochemical/biophysical studies allow us to draw certain conclusions about interactions. With detailed investigations, collected data may even allow us to draw a fairly accurate picture concerning the molecular basis of physiological changes which contaminants are able to induce.

Admittedly, investigations such as these are difficult to perform. The molecular complexity of living systems defies ready characterization, and it is even more difficult to relate alterations in molecular organization to the subsequent physiological changes wrought by this contaminant-host interaction.

Recent years have seen an upsurge of interest in membranes and how membrane structure is modified when invaded by such things as drugs and insecticides. The reasons are several: membranes house cells, control the influx and efflux of nutrients and metabolites; membranes control and form the basis for the transmission of electrical signals (nerve impulses) when nerve receptor sites are stimulated. Any major alteration to normal membrane structure may be expected to play some role in animal physiology, especially if the contaminated membrane is associated with neural function or other viable life processes.

Membranes consist of a sandwich of phospholipids, sterols, and proteins; individual membranes are microscopically thin. The thinness and complexity of membranes make their study most difficult. One way of characterizing membranes is by measuring their electrical properties (conductance, resistance, capacitance, etc.). However, with respect to contaminant-host interaction, it is more desirable to be able to deduce structural features such as lipid fluidity, protein-lipid interaction, and arrangements of constituents in dynamic tissue preparations. This, then, precludes the use of electron microscopy or other methods which are incompatible with maintaining tissue in a viable unchanged condition.

THE THEME OF THIS REPORT—SPIN-LABELING

Several years ago, it was observed that certain free radical derivatives of fatty acids could be introduced into membrane preparations without unduly disturbing the natural arrangement of native membrane constituents (Jost et al. 1971). Furthermore, it was shown that these free radicals would associate with and align in membranes

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much the same way as do the nonradical natural fatty acids present in membranes (Libertini et al. 1969; Hubbell and McConnell 1969; Schreier-Muccillo et al. 1973). By using appropriate instrumentation, it was found that these radicals could be used as submicroscopic probes (or labels) for investigating membrane structure. This has become known as spin-labeling, and forms the underlying theme of this paper. This report describes our work on contaminant-host interaction in fingerling salmon. To show how these studies were performed, we need to arm ourselves with some basic background information. Let us review briefly some very important points concerning radicals, electrons, and nuclei.

THE FOUNDATION OF SPIN-LABELING

Free Radicals

Many free radicals are known or have been isolated. Most, as we know, are quite reactive chemically, and unless conditions conducive to their formation and stabilization (trapping) are maintained, radicals normally disappear once formed. Radical reactivity stems from the fact that radicals, by definition, are molecules which contain one or more unpaired electrons. Two radical partners normally pair together to yield end products with the normal complement of two electrons per chemical bond. This is the usual covalent bond and is characteristic of organic compounds.

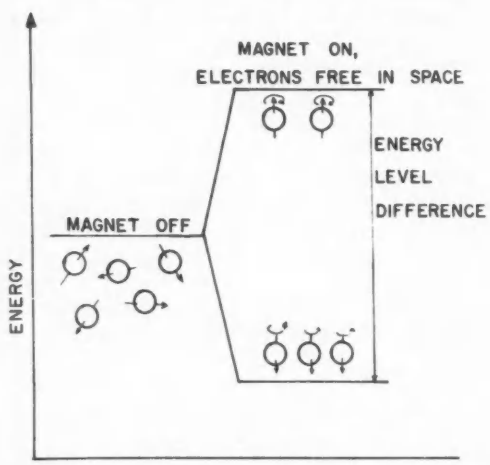

FIGURE 1.—Resonance condition for isolated electrons. In the absence of external field, energy levels are indistinguishable. When a magnetic field is applied, two levels (and only two levels, by quantum mechanical restrictions) are populated by electrons. By employing X-band microwaves (9 GHz) with the proper energy ($h\upsilon = g\beta H$; see for instance, Roubal 1972), flipping between levels occur and the absorption of microwave energy is observed.

There is one class of free radicals, the nitroxides, which are stable under many of the usual laboratory conditions. Nitroxide stability derives from resonance and other contributing factors, but we need not discuss these here. Many nitroxides are relatively easy to synthesize, provided the necessary starting intermediates (some of which are rare) are at hand.

The important point to be made is the fact that nitroxides can be used to characterize biological systems. Nitroxides so used are called spin-labels; *spin* from the fact that it is the unpaired electron(s) (which is/are spinning) which forms the basis for the *label* or probe. Spin-labeling might just as conveniently be called spin-probing.

Spinning Electrons and Their Magnetic Properties

All electrons are in a state of motion; they all spin about on their axis. Spinning electrons are therefore moving charges of electricity. Thus electrons are magnetic. Spinning electrons therefore are influenced by an external magnetic field such as produced by a solenoid or electromagnet. When a sample of free radicals is placed between the poles of an electromagnet, the spin of the electron is described as clockwise or counterclockwise and is depicted in Figure 1.

Of immediate consequence is the fact that one spin condition is more stable than the other, and is so indicated by the reference to the energy of the system as shown. Although one population level is more stable than the other, the temperature of the system is always great enough to insure that the higher level contains just about as many electrons as the lower level. This is something akin to placing two bar magnets end to end. If they are aligned N-S N-S, we know from everyday experience that the interaction will be attractive and stable. If, on the other hand, we try to force them N-S S-N, we know again from experience that this is an unstable situation and requires an expenditure of energy (heat in the case of electrons, physical in the case of magnets) to maintain

them aligned in this fashion. Apart from this, however, the analogy extends no further, for in the realm of electrons and nuclear phenomena, quantum mechanical postulates hold and the common experience of our everyday world does not pertain.

The important point we want to make here is that we can induce an electron with one spin rotation to flip over and assume the alternate rotation. Energy is required to do this. To achieve flipping, the sample is irradiated (while between the poles of the electromagnet) by microwaves with a frequency of 9 gigahertz (GHz). Thus we see that what we are really talking about is just another type of spectroscopic method. The presence of free radicals is detected by measuring the loss of microwave energy. The actual instrument used for such studies is called the electron paramagnetic resonance (EPR) spectrometer (also called the electron spin resonance/ESR/spectrometer).

At this point we must consider other factors which contribute to the total magnetism of the system. Remember that the unpaired electron is not merely floating freely about in space. It belongs to a molecule. In fact it is coupled to a nucleus, and in the case of nitroxides, to a nitrogen nucleus, which is itself a magnetic entity. Thus in the presence of an external field, the nuclear magnetism can couple with the external field and alter the magnetism immediate to the electron. We must now consider this situation, called hyperfine splitting (hfs).

Hyperfine Splitting (hfs)

Simply stated, it is found that the nitrogen magnetism can add to, subtract from, or be orthogonal (no interaction) to the external field. This is depicted in Figure 2.

Note that the situation of Figure 1 is now modified. The original resonance (flipping) condition is broken down into three resonances (hfs). The flipping from one level to the other is depicted by the double ended arrows A, B, and C. Certain restrictions are placed on flipping, and we find that only those shown are allowed. All levels are equally populated, and an actual EPR spectrum of a nitroxide in dilute solution is shown in Figure 3.

Spin-Label Spectra

While the spectrum of Figure 3 tells us most conclusively that we are dealing with a nitroxide,

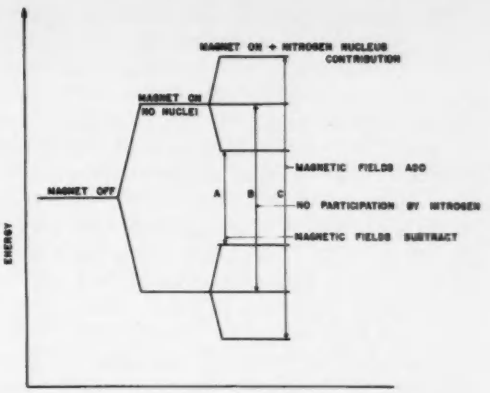

FIGURE 2.–Resonance condition for the case of one electron interacting with a nitrogen-N^{14} nucleus. Due to quantum mechanical restrictions, only those transitions shown are allowed.

it serves no further purpose other than a possible quantitation of the amount of radical (number of spins) present. If all we ever measured were three sharp, hyperfine lines, we could not use nitroxides as spin-labels.

Fortunately, when a nitroxide is placed in an actual biological system, the hyperfine lines are modified both in shape, intensity (relative height), and in spacing. These spectral modifications are environment dependent, and it is this dependency which makes nitroxides valuable as probes for characterizing biological systems.

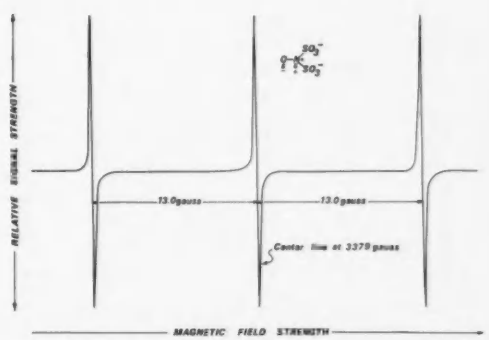

FIGURE 3.–EPR spectrum of the nitroxide compound potassium peroxylamine disulfonate (Freemy's salt) (10^{-3}M) in water at room temperature. Three hyperfine lines of equal intensity, and spaced 13 gauss apart, distinguish nitroxides in water.

It is sufficient to simply state that the unpaired electron is localized on nitrogen and this localization resides primarily in a p-orbital on nitrogen. p-Orbitals are dumbbell-shaped electron density regions in space, and the magnetic properties associated with an electron in such an orbital depends on the so-called tumbling frequency of the electron (how fast the p-orbital assumes a random distribution of orientations while part of the nitroxide in a biological system). An example of two limiting situations is shown in Figure 4. Spectrum 4A was recorded for a nitroxide in liquid glycerol, while 4B is for the frozen solution. Spectrum 4A tells us that moderate fast tumbling prevails, while 4B shows tumbling to be essentially quenched. The reader is referred to the literature (Roubal 1972) for a more thorough discussion on the dependency of spectral characteristics on tumbling frequency (label mobility).

Intermediate mobilities are characterized by a family of spectra. Examples are to be found in the recent spin-labeling study of a hapten combining site of trout antibody by Roubal et al. (1974). Using appropriate mathematical manipulations of recorded spectra, one can measure tumbling frequencies with accuracy. These frequencies together with other derived data provide quantitative characterization of labeling studies.

MEMBRANES AND MEMBRANE PROPERTIES

The importance of membranes in biological roles of living systems cannot be overemphasized. Membranes, as mentioned, are responsible for neural function. Membranes participate in ion-binding and in governing tissue permeability. Associated with membranes, especially mitochondrial membranes, are a variety of enzymes. Cytochrome oxidase and other electron transport enzymes are membraneous in nature. Membrane-bound enzymes require the proper conditions such as lipid fluidity, proper phase transition temperatures, and lipid-protein interactions for their function. The participation of membranes in neural control is well documented. Neural membranes contain molecular size pores which mediate sodium/potassium transport. The exact nature of these pores has not been delineated completely, but several lines of evidence suggest that pores consist of a cagelike arrangement of protein which spans the membrane from the inner to the outer surface. Membranes are considered to be the basis of life itself.

Membranes consist principally of proteins and lipids. Carbohydrates comprise 0-10% of the membrane mass. Lipids account for about 40% of the mass, and the balance is protein. Membranes are a matrix of lipids and proteins arranged in a bimolecular leaflet (Singer 1972; Green 1972), illustrated in Figure 5. The little circles represent phospholipid headgroups (choline, ethanolamine, serine, phosphatidic acid, etc.) while proteins are indicated by the larger "islands." Interspersed with the fatty acid tails (squiggly lines) are sterols and lesser tissue lipid components. Typical membranes are about 100 Å thick.

Membrane lipids are amphiphilic—provided

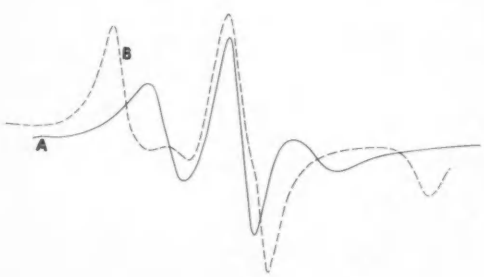

FIGURE 4.—Label II (see text) in glycerol.
A. In liquid glycerol at room temperature.
B. Frozen in glycerol at liquid nitrogen temperature.
Label mobility (effect of environment) is calculated by measurements of line widths, heights, intensity ratios, and spacing.

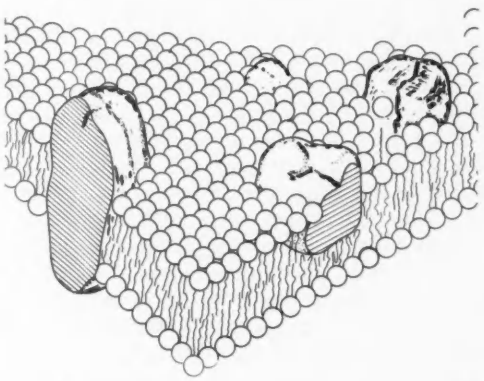

FIGURE 5.—Membrane bilayer leaflet. Small circles represent phospholipid headgroups. Squiggly lines are fatty acid tails. Large islands represent membrane protein. From Singer 1972. (Courtesy of S. J. Singer and New York Academy of Sciences.)

with polar headgroups and nonpolar tails of carbon-hydrogen chains. Thermodynamically, and for other reasons as well, the greatest stability for membrane structure results when membrane constituents are arranged as shown; polar surfaces are exposed to aqueous environments, and the fatty acid tails are tucked away out of contact with water.

QUESTIONS ABOUT CONTAMINANT-HOST INTERACTION

We would like to answer the following questions concerning membrane-contaminant interaction: a) are certain regions of membranes affected or is the whole membrane affected when invaded by contaminant? b) if the effect is localized, where is the localization? c) are there differences in membrane perturbations when treated on the one hand by paraffins, and aromatics on the other? d) can the differences, if they exist, be related to anything presently known about the toxicology of any of these contaminants?

EXPERIMENTAL METHODS AND RESULTS

The study was performed in two steps. First, an in vivo feeding study was undertaken. Here we used spin-labeled hydrocarbons (Roubal 1974) and fed them to fish. Second, an in vitro study was employed using excised tissue. In order to restrict our investigations of membranes (in vitro) to specified regions, the series of labels I, II, and III (Roubal 1974a) (Figure 6) were synthesized by the EPR group of this Center. The positively charged quarternary nitrogen of label I directs this portion of the label to the polar membrane surface, which in turn insures that the nitroxide nitrogen is situated at or very near to the membrane surface. The carboxyl groups of labels II and III direct the carboxyl end of these amphiphiles to the membrane surface, but now the nitroxide nitrogen lies some 12-15 Å below the membrane surface in II, and deep into the hydrophobic membrane interior in III. Thus we can "look" at the membrane's surface, subsurface, and interior.

In the feeding study, spin-labeled hydrocarbons were incorporated into fish food and fed to coho salmon, *Oncorhynchus kisutch*, fingerlings in a 2-day feeding study. Within an hour, or even less, after onset of intake of food by fish, the blood showed EPR activity. Using radiotracers, we have shown this activity to be associated with blood lipoproteins and albumins (Roubal 1974b), with lipoproteins making the greatest contribution to hydrocarbon transport in blood.

After an induction period of about a day, blood-associated labels (Roubal 1974b) slowly transfer to neural tissue and flesh. Weight for weight, the greatest concentrations are to be found in the spinal cord, lateral line nerve bundles, and brain. The nature of the EPR line shapes indicated that the invasion of hydrocarbon is site selective. All labeled paraffins appeared to intercalate with membrane in such a way that the nitroxide mobility is little impeded. In direct contrast to this, mobility of aromatics appeared to decrease. This in vivo study suggests that paraffins associate with molecularly fluid portions of membrane fatty acids, while aromatics associate with the more structured and rigid regions of membranes. In order to clarify these possible differences, an in vitro study was undertaken using labels I, II, and III (Roubal 1974a).

Neural tissue from untreated fish was carefully excised and placed in cold, 0.1 M phosphate buffer, pH 7.4 at 4°C, isotonic in NaCl. A sonicated dispersion of label, complexed to bovine serum albumin was added and allowed to transfer to neural membrane (overnight at 4°C). Membranes were then inserted directly into the EPR spectrometer, and the spectra were recorded immediately. After

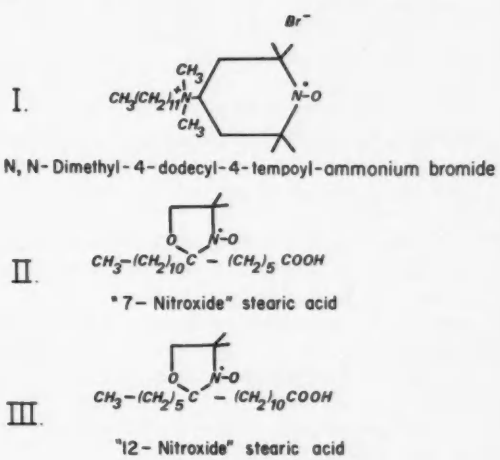

FIGURE 6.—Lipid-intercalating spin-labels.
Label I reports on surface conditions.
Label II reports on subsurface conditions.
Label III reports on interior conditions.

the spectrum for one sample was obtained, the tissue was returned to a large volume of fresh, cold buffer to which test hydrocarbon (in separate tests) was incorporated via sonication. Final hydrocarbon concentration in buffer was 15-25 ppm. Hydrocarbons included benzene, toluene, ethyl benzene, hexane, heptane, octadedecane, and cyclohexane. Actual uptake of paraffin hydrocarbon by tissue membrane, as measured by gas-liquid chromatography (GLC), was on the order of 1 ppm. Aromatics were present in higher amounts (5-10 ppm). Tissue was exposed to hydrocarbon in buffer for 1 h. At the end of this period, tissues were withdrawn, rinsed well, and the EPR spectra were re-recorded.

A comparison of the in vitro spectra for controls with those same samples after hydrocarbon treatment provided evidence that a differentiation in binding sites for paraffins and aromatic compounds does indeed exist (Figure 7).

DISCUSSION

We can explain rather easily the preference of paraffins seeking the interior of membranes—paraffins are nonpolar, very soluble in neutral hydrocarbons, such as those which comprise the hydrogen-carbon chains (or tails) of phospholipid fatty acids. Hence, thermodynamically, system stability is enhanced by mutual interaction of paraffin hydrocarbon with lipid tails.

Aromatics, on the other hand, are unique, for in addition to their ready solubility in many organic environments, aromatic compounds are fashioned from conjugated double bond systems with pi-electron unsaturation. These factors give aromatics the ability to form quasi-chemical complexes with other molecules which can act in electron acceptor-donor roles.

The surface of the membrane contains many different sites, both polar, nonpolar, and electron-interactive. It appears that some of these sites contain the necessary properties which make binding of aromatics possible. A charge-transfer mechanism (Kier 1971) may direct aromatics away from the membrane interior to the surface.

These site preferences for paraffins and aromatics may account in part for the differences we observe for retention of these substances in living tissue. For instance, in other studies (Roubal 1974b) we have shown via GLC, spin-labels, and radiotracers that paraffins are retained in living tissue for long periods of time; aromatics are not. What is more, paraffins are relatively nontoxic, while aromatics generally are quite toxic, even at low levels.

The molecular basis for physiological phenomena is associated in a very direct way with important membrane properties. Ion-binding, lipid protein (enzyme) interaction, lipid phase-transition temperatures, and lipid fluidity are all involved in one way or another. Membrane disor-

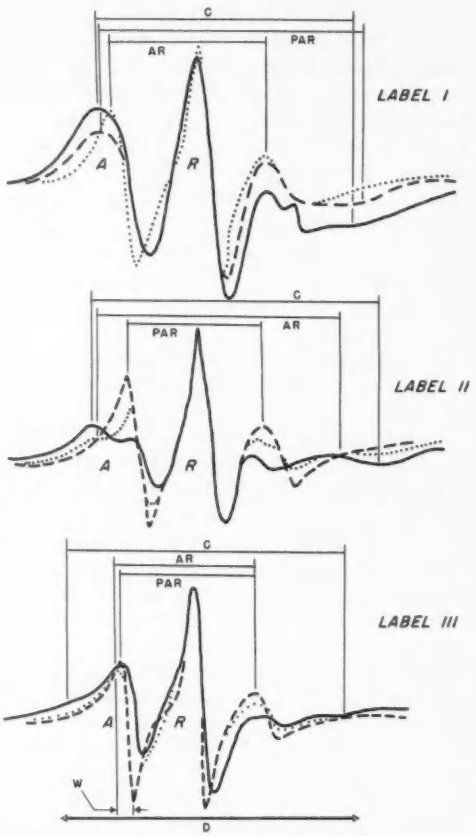

FIGURE 7.—Spin-label spectra of aromatic-treated and paraffin-treated coho salmon spinal cord (SC).
SC + Label I (+ treatment).
SC + Label II (+ treatment).
SC + Label III (+ treatment).
Changes in the A/R (line height) ratio, narrowing of peak widths (W), and shifts in distance D to lesser values provide data for characterizing influence of treatments (Roubal 1972; Roubal 1974a). C, spinal cord control.
AR, treatment by aromatics.
PAR, treatment by paraffins.

ganization is considered to involve alterations in these properties. Accordingly, on invasion of membrane primarily by aromatics, surface perturbations as indicated by spin-labeling spectra reflect changes in ion-binding properties of phospholipid headgroups, enzyme activity, and permeability changes.

From the standpoint of membranes, paraffins are tolerated up to a point, by shunting them into internal reaches of membrane, away from active metabolic processes. Our spin-labeling studies show lipid fluidity to be altered when tissue is exposed to paraffins. These changes are rather diffuse, however, and not associated with any one portion of the membrane interior. Such alterations however, could be operative in altering ion transport.

We contend, therefore, that aromatic-membrane interaction is of paramount concern. This is especially true when behavioral/physiological patterns are to be explained. Additional insight into these areas will necessitate further biophysical studies—both spin-labeling and broad-based electrophysiological studies.

FUTURE OUTLOOK ON SPIN-LABELING

Spin-labeling was first described only as recently as about 1968. Since then, a vast array of labels have been described. New instrumentation has evolved, and the technique has grown from a tool of limited application to one of major importance. For many biochemical and biophysical studies, the technique stands prominently above other methods. Applied to drug studies, pharmacology, immunology, cancer research, enzymology, and protein structure studies, spin-labeling promises to play an ever growing role. Environmentalists, biologists, zoologists, and food scientists now apply this tool to their studies. The future of spin-labeling is bright indeed.

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TELECONNECTIONS BETWEEN NORTHEASTERN PACIFIC OCEAN AND THE GULF OF MEXICO AND NORTHWESTERN ATLANTIC OCEAN

JAMES H. JOHNSON AND DOUGLAS R. MCLAIN[1]

ABSTRACT

Anomalous large-scale air-sea interactions that took place over the Gulf of Mexico and the Atlantic Ocean off the southeastern coast of the United States in the winter of 1957-58 caused a change of sea-surface temperatures from near average values to cold anomalies of nearly 3.0°C in some regions. Evidence suggests that the mechanism for the anomalous change in sea temperatures derived from frequent outbreaks of cold, North American continental air flowing over the Gulf and ocean waters with consequent anomalously high evaporation and sensible heat exchange. A contributing factor may have been divergence of surface waters with associated upwelling in regions of high cyclonic activity.

These severe outbreaks of cold continental air over the eastern seaboard may be related to air-sea interactions in the Pacific, thousands of miles distant. It is not clear what the full consequences of these events are to fisheries. The evidence which is available suggests that they are significant and warrant continued investigation.

In recent years large-scale air-sea interactions have captured the interest of a number of oceanographers and meteorologists. Motivated by the desire to develop and improve extended meteorological forecasts, Namias (1959, 1963, 1972, and in numerous other articles) has been one of the foremost investigators in studying these interactions. Most of his work has centered in the temperate latitudes of the northern hemisphere. Bjerknes (1966a, b, 1969) has studied large-scale interactions in the tropical Pacific Ocean, especially, processes associated with the El Niño phenomena. He has shown a relationship of fluctuations in the atmospheric Hadley circulation to large-scale anomalies of ocean temperatures. He suggests that an anomalously high heat supply in the equatorial Pacific, characterized by high equatorial ocean temperatures, intensifies the Hadley circulation providing more than normal flux of angular momentum to the mid-latitude belt of westerly winds, thus affecting the weather over the North American continent. He suggests that regular monitoring of sea temperatures in the eastern tropical Pacific is indispensable in long-range weather forecasting for North America.

Also motivated to develop improvements in long-range weather forecasting, Quinn (1972) has shown that large-scale interactions over the equatorial Pacific may affect the weather over the continental United States. He suggests that extensive dry-zone developments in the equatorial zone, which are associated with low sea-surface temperatures, may contribute to ridge development in the upper air circulation over the Northeast Pacific and, conversely, wet-zone developments (high equatorial sea temperatures) are associated with trough formation. Furthermore, he describes the effects downstream over the United States following development of these troughs and ridges and implies that now it may be possible, if these extreme developments are detected early enough, to make long-range weather predictions over North America.

Rowntree (1972), recently carrying out computer model studies, has confirmed that a sea temperature maximum in the tropical eastern Pacific leads to a persistent trough in the mid-latitude flow to the north.

Regions of the ocean particularly responsive to the overlying atmosphere lie to the east of large continental land masses. Jacobs (1951), Manabe (1957), Wyrtki (1966), and Hishida and Nishiyama (1969) have shown that in wintertime the temperate western Pacific Ocean loses large amounts of heat through evaporation and sensible heat exchange because of the overflow of cold, dry Siberian air masses. Parker (1968) pointed out a similar effect in the winter of 1966 in the northwestern Gulf of Mexico.

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This paper extends the findings of several of the authors mentioned above by describing the development of large-scale sea-surface temperature anomalies in the winter of 1957-58 in the Gulf of Mexico and off the U.S. eastern seaboard and suggests that these anomalies are associated with ridges and troughs in the upper air circulation. These, in turn, are associated with air-sea interactions in the Pacific. It further describes conditions in other winters where similar situations developed and suggests that changes in abundance and distribution of some fish populations both in the Pacific and Atlantic may be caused by events of this nature.

DATA SOURCES

Data used in heat budget calculations and in the description of sea-surface temperatures and anomalies were obtained from Tape Data Family 11 obtained by Fleet Numerical Weather Central and the Navy Oceanographic Office from the National Climatic Center, Asheville, N.C. This file contains merchant ship weather reports, some of which date back to 1854. Computer programs were developed to compute monthly averages by year of sea-surface temperature and heat exchange by 5° blocks.

Numerous studies have been made to determine the accuracy of sea-surface temperatures reported by merchant vessels in their weather reports. Saur (1963) found that in the Pacific the average injection temperature bias from that of a bucket temperature taken at the surface was about +1.2°F, and Franceschini (1955) noted similar results in the Gulf of Mexico. The latter suggested, however, that commercial vessel reports could be used for practical purposes such as meteorological and oceanographic research and for forecasting air mass modification over the Gulf. Because uncertainties remain concerning the relation between temperature at the sea surface and that at the injection intake depth of merchant vessels, no attempt was made in this study to apply a correction.

OBSERVATIONAL EVIDENCE OF ANOMALOUS AIR-SEA EVENTS

The Anomalous Winter of 1957-58

Charts of the height of the 700-mb (millibar) pressure surface (on the average about 10,000 feet above the surface of the earth in temperate latitudes) are particularly significant in air-sea interaction studies because the mass circulation of the atmosphere can be inferred from them including areas of cyclogenesis and movement of storms. Furthermore, mean 700-mb heights over the ocean are highly correlated with 700-mb temperatures, which in turn are measures of the vertical stability in the atmosphere over the ocean. For example, low temperatures at the 700-mb level, associated with negative 700-mb height anomalies, indicate instability in the atmosphere and loss of heat from the ocean through convective processes in the atmosphere.

O'Connor (1958) reported that the heights of the 700-mb surfaces during the winter of 1957-58 were very unusual. He reported the following three abnormalities in the 700-mb circulation in January 1958 (Figure 1) which persisted into February:

1. A trough in the east-central Pacific with 700-mb heights 550 feet below normal 700 miles south of Kodiak, Alaska,
2. A block in the Davis Straight where the 700-mb heights averaged 520 feet above normal and,
3. A trough in the southeastern United States (having 700-mb heights about 300 feet below normal) accompanied by strong northerly surface flow.

The trough along the eastern seaboard is particularly important. It suggests greater than normal penetration of cold continental air masses over the southeastern United States and adjacent waters. Indeed, the winter of 1957-58 will be remembered as one of the most severe of the century. Data taken at National Weather Service stations in the southeastern United States show slightly higher than normal air temperatures in November 1957 (Table 1). A small negative anomaly developed in December which increased substantially in January 1958 and reached a maximum in February. Monthly deviations of air temperature ranged up to 5.8°C below normal at stations along the northeast coast of the Gulf of Mexico.

Large negative sea-surface temperature anomalies also prevailed in February 1958 and were greatest in the northeastern Gulf in the same general area where shore station air temperature anomalies were highest (Figure 2). Stearns' (1964,

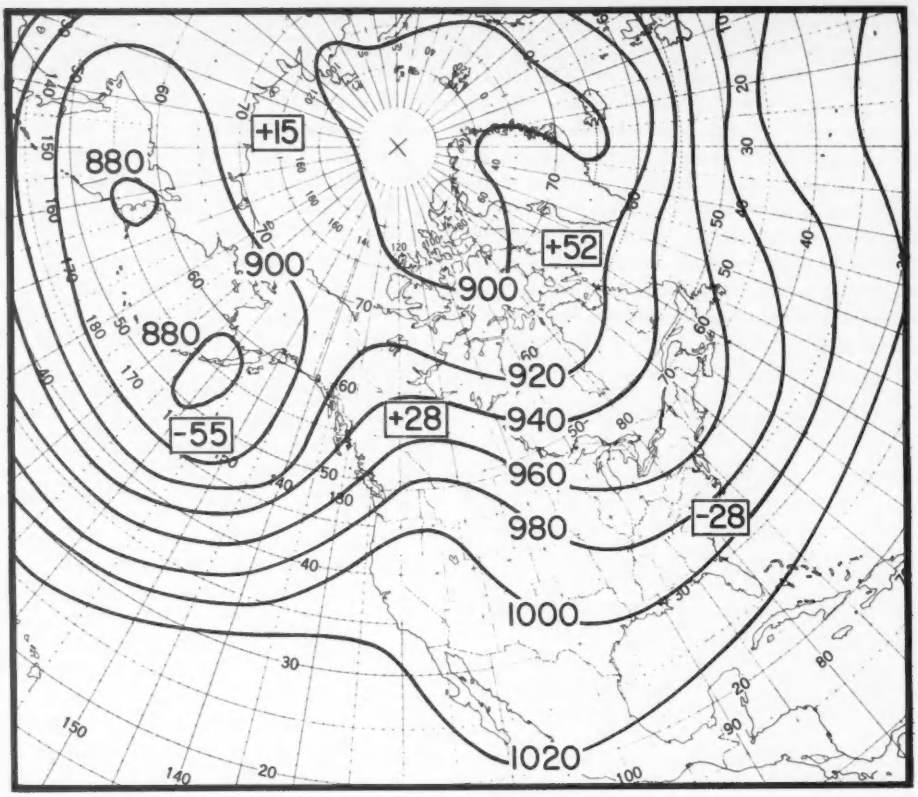

FIGURE 1.—700-mb heights and departures from normal, tens of feet, January 1958. Major departures are enclosed in boxes.

TABLE 1.—Monthly average air temperatures (°C) and departures from average (°C), November 1957-March 1958 at selected National Weather Service Stations.[1]

Station	November 1957		December 1957		January 1958		February 1958		March 1958	
	Temperature	Departure	Temperature	Departure	Temperature	Departure	Temperature	Departure	Temperature	Departure
New York, N.Y.	9.6	+1.6	4.8	+2.7	0.0	−0.4	−2.6	−2.8	4.5	−0.3
Wilmington, Del.	8.1	+0.6	3.3	+1.6	−0.7	−1.4	−2.6	−3.6	3.9	−1.9
Wilmington, N.C.	13.4	+0.2	9.6	+0.4	4.9	−3.8	4.9	−4.3	9.5	−3.1
Charleston, S.C.	15.4	+0.6	10.9	−0.3	7.0	−4.1	6.5	−5.0	11.8	−2.7
Savannah, Ga.	15.0	+0.8	10.3	−0.6	6.6	−4.3	6.8	−5.1	12.2	−2.6
Jacksonville, Fla.	18.5	+2.1	12.1	−1.5	9.1	−4.1	9.0	−5.2	15.1	−1.7
Miami Beach, Fla.	24.1	+0.8	19.9	−1.7	17.7	−3.4	16.6	−4.6	22.0	−0.3
Key West, Fla.	25.2	+1.6	20.3	−1.8	18.5	−3.0	17.5	−4.5	21.3	−1.8
Fort Myers, Fla.	22.0	+1.3	16.5	−2.1	13.9	−4.2	13.1	−5.6	18.8	−1.5
Pensacola, Fla.	16.2	+0.6	11.9	−0.9	8.3	−3.9	7.6	−5.7	14.3	−1.4
Mobile, Ala.	15.2	+0.4	11.2	−0.7	7.3	−4.2	6.9	−5.8	13.6	−1.6
New Orleans, La.	16.5	+0.5	12.9	−0.5	9.8	−3.5	9.1	−4.9	15.3	−1.7
Galveston, Tex.	17.2	−0.3	14.9	+1.3	10.7	−1.7	10.4	−3.6	14.3	−2.3
Corpus Christi, Tex.	17.3	−0.9	16.4	+1.5	12.8	−1.1	13.9	−1.8	15.7	−2.8

[1]Source: Local Climatological Data reports, U.S. Department of Commerce, National Weather Service.

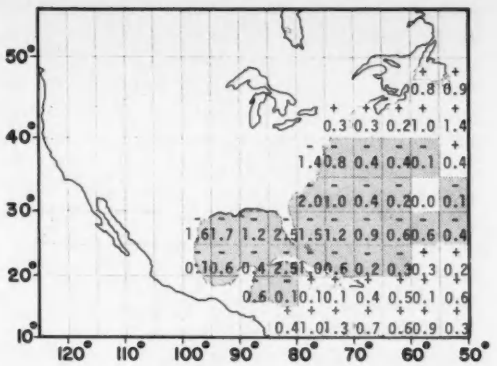

FIGURE 2.—Sea-surface temperature anomalies (°C) Gulf of Mexico and western Atlantic Ocean, February 1958. Shaded area colder than 20-yr (1948-67) mean.

1965) analysis of sea temperatures at coastal stations confirm the large winter sea temperature anomaly in coastal areas of southeastern United States. The extent of the anomaly was large, indeed, extending from below the Yucatan Straits northward throughout the Gulf to lat. 40°N off the eastern seaboard and to over a thousand miles offshore.

Important in this study is the anomalous change in sea temperatures in the winter of 1957-58 (Figure 3). The change from November to February shows that much higher than average cooling occurred over a broad expanse of the ocean during this winter. For example, the 1948-67 average change in sea-surface temperature in winter (November average - February average) is

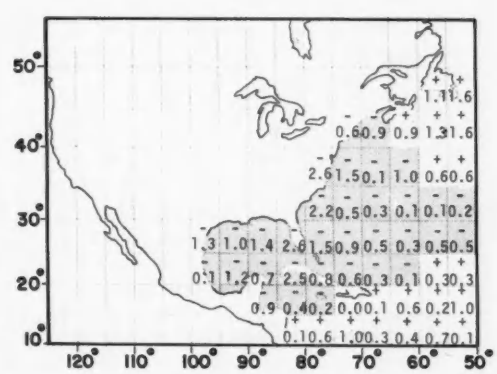

FIGURE 3.—Anomalous sea-surface temperature change (°C) November 1957 to February 1958. Shaded area indicates anomalous cooling.

about -2.7°C in the area lat. 25° to 30°N, long. 80° to 90°W. In the winter of 1957-58, however, the change in this area was -4.7°C—an anomalous change of -2.0°C.

Cause of Sea-Surface Temperature Change in the Winter of 1957-58

A variety of processes can cause changes in sea-surface temperatures. Some of these are horizontal and vertical advection and heat exchange at the air-sea interface.

In studies in the eastern Pacific Ocean, Clark (1972) has found that horizontal advective heat transfer processes in winter and spring have a greater effect in causing anomalous sea-surface temperature change than nonadvective processes. The latter have a greater effect in summer and fall. The area that he studied, however, was not subject to influence of a large continental land mass interacting with atmospheric circulation upstream from where heat exchange processes were calculated.

Horizontal advection into the Gulf of Mexico is mainly through the Yucatan Straits. Sea-surface temperature anomalies in these Straits ranged from -0.2°C to +0.4°C (Table 2) for a year preceding the maximum development in February 1958 of the severe cold anomalies in the Gulf of Mexico and along the eastern seaboard. This clearly suggests that horizontal advection was not the cause of the development of the cold anomalies.

Klein (1958) noted that the intensification of blocking in the 700-mb circulation in the northwest Atlantic in the winter of 1957-58 was associated with frequent outbreaks of cold air in the

TABLE 2.—Sea-surface temperatures and anomalies (°C) in 1° square (long. 85° to 86°W and lat. 21° to 22°N) in Yucatan Straits.

Date	Sea temperature °C	Anomaly °C
1957:		
January	26.2	−0.2
February	26.6	+0.3
March	26.4	−0.1
April	27.0	+0.1
May	28.0	+0.2
June	28.7	0.0
July	29.3	+0.1
August	29.7	0.0
September	29.5	−0.1
October	28.8	−0.2
November	28.0	0.0
December	27.5	+0.4
1958:		
January	26.2	−0.2
February	25.6	−0.7

eastern two-thirds of the United States. The contrast between this cold air and the air heated by the Gulf of Mexico and western Atlantic waters led to baroclinic deepening of coastal storms. In these regions of cyclonic activity, vertical advection may have caused some cooling through divergence of surface water and consequent local upwelling. Leipper (1967) has shown that hurricane Hilda, passing over the Gulf of Mexico in the early fall of 1964, indeed did cause significant cooling of surface waters through upwelling processes. However, the large area covered by anomalously low sea-surface temperatures in the winter of 1957-58, and other factors such as the frequent cold outbreaks over the entire eastern seaboard and the fact that the sea temperature anomalies appeared to occur over large areas contemporaneous with the overflow of cold air, suggests that the high rate of sea surface cooling was due to anomalously high loss of heat through evaporation and conduction of sensible heat.

To test this supposition formulae for calculation of the heat exchange at the air-sea interface have been employed. Laevastu (1965), Seckel (1962) and many others have provided these formulae. In this study the procedures for calculation of the energy exchange as presented by Johnson et al. (1965) are used. It is not the intent here to review the accuracy of the various techniques for estimating air-sea energy exchange. Because of the possible inaccuracies of input data and of the formulae, the exchange values should be viewed with caution and should be considered only as relative indices of the magnitude of energy flux at the air-sea interface. They appear, however, to be sufficiently accurate to permit detection of large-scale seasonal and nonseasonal variations.

The equation for the heat exchange at the air-sea interface is

$$Q_T = Q_I - Q_R - Q_B - Q_E - Q_H$$

where:

Q_T = Net heat gained or lost at the sea surface
Q_I = Incident solar radiation corrected for cloud cover
Q_R = Reflected radiation
Q_B = Back radiation
Q_E = Evaporation
Q_H = Conduction of sensible heat.

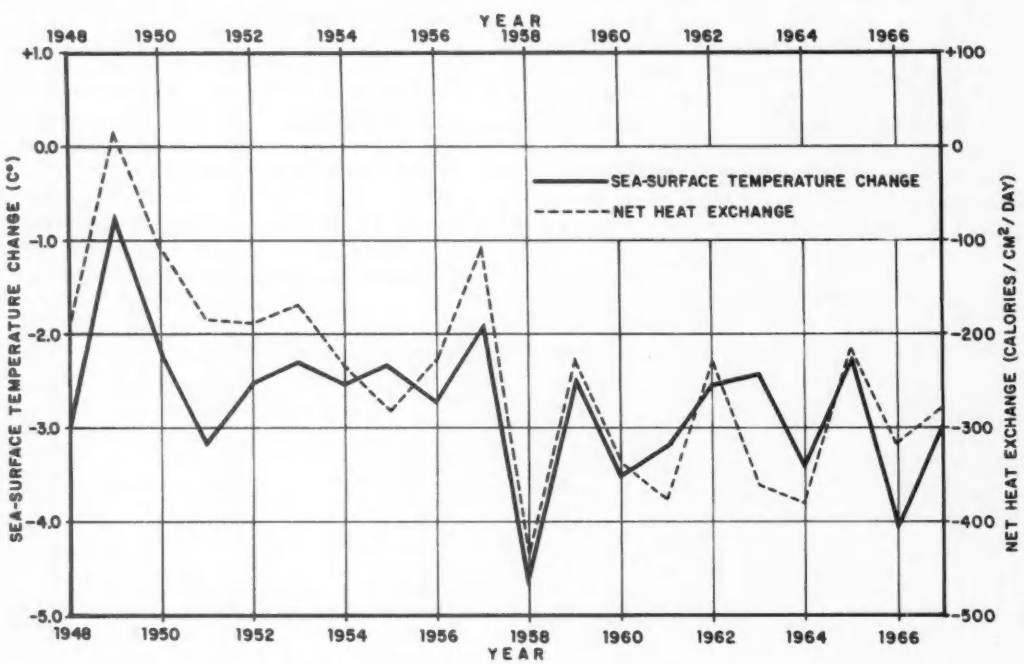

FIGURE 4.—Relation between net heat exchange at air-sea boundary and sea-surface temperature change winters of 1948-67 in the area bounded by long. 80° to 90°W and lat. 25° to 30°N.

The relation between Q_T and sea-surface temperature change in the winters of 1948-67 in the northern Gulf of Mexico is significant (Figure 4). Particularly noteworthy is the large net heat loss in the winter 1957-58 accompanied by the large sea-surface temperature change. The decrease in Q_I reaching the sea surface accounted for about 11% of the anomalous heat loss and increased Q_B about 12%. Q_E and Q_H, however, clearly stand out as significantly more important than the other heat budget elements in contributing to the large net loss of heat. Q_E contributed 57% of the anomalous heat loss and Q_H, 20%.

Data are not available that indicate the depth to which the sea temperature anomaly extended. One might speculate that it should extend throughout the mixed layer which on the average in the area of study is about 80 m in winter (Robinson 1973). For the three months December 1957-February 1958, the anomalous heat loss in the Gulf of Mexico in the area of lat. 25° to 30°N, long. 80° to 90°W was approximately 19,000 cal/cm^2. This should reflect an anomalous change in water temperature of about -2.4°C throughout the mixed layer which is very close to the anomalous -2.0°C change observed at the surface.

Though the immediate cause of the development of the cold anomaly appears to have been the flow of cold continental air over the Gulf and western Atlantic, the more general cause may have been due to large-scale interactions over the North Pacific Ocean. A large positive sea temperature anomaly appeared in the eastern Pacific in late 1957 and persisted throughout 1958 (Sette and Isaacs 1960) (Eber 1971). Namias (1959) explains that the contrast of anomalous warm ocean temperatures to the east of cold ocean temperatures, which was the situation in 1957 in the eastern Pacific, provided abnormal feedback in heat exchange processes to the atmosphere which provided the additional baroclinicity upon which cyclones could feed. This cyclogenesis helped maintain the deep Pacific trough south of Kodiak Island which was abnormally intense by the late fall of 1957. Downstream from this area of activity, a responsive ridge developed in the western United States (evident from Figure 1) and a deep trough along the Atlantic seaboard. This distribution is also consistent with the statistical findings of O'Connor (1969) who noted that when an anomalously deep trough forms in the 700-mb circulation in the east central Pacific, the chances for a trough off the eastern seaboard are high.

Air-Sea Interactions in Other Years

It is tempting to argue that events such as the 1957-58 occurrence described above occur so seldom that it is not worth the effort to study them and their effects on fisheries. Study of years when extreme conditions prevail, however, provides hints of the processes that are occurring in the natural system in other years. Definitive findings through study of more normal years are often difficult to obtain because processes involved may be obscured by the subtle interactions of a number of factors.

The interaction of the type described above may not be as infrequent as one might believe. A situation similar to the winter of 1957-58 seems to have occurred in the winter of 1939-40. O'Connor (1958) noted very cold air temperatures along the eastern seaboard in the winter of 1939-40 which were as intense as those in 1957-58. Although sea temperature records are sparse for winter months (December through February) of 1939-40, what data are available show an extremely cold and widespread anomaly in the Gulf of Mexico (Figure 5) and along the eastern seaboard where temperature anomalies of 5° and 6°C below normal were observed in February 1940.

Further analysis of these large-scale air-sea interactions suggest a possible relation between equatorial Pacific Ocean temperatures and those in the Gulf of Mexico. Bjerknes (1969) has shown that in the winters 1957-58, 1963-64, and 1965-66 high sea-surface temperatures prevailed in the eastern tropical Pacific Ocean. This is characteristic of El Niño years which are best known for the invasion of warm water off the Peruvian coast and effects on the anchoveta populations there. It is known also that in the winter of 1939-40 a severe El Niño was present in the eastern Pacific. In all of these winters cold sea-surface temperature anomalies prevailed in the Gulf of Mexico (Figure 5). There appears, then, to be a relation between sea temperature anomalies in the equatorial Pacific and anomalies in the Gulf of Mexico, that is, negative sea-surface temperature anomalies in the Gulf and western Atlantic in some situations may be related to positive sea temperature anomalies in the eastern equatorial Pacific through processes described by various authors mentioned previously and those described in this paper.

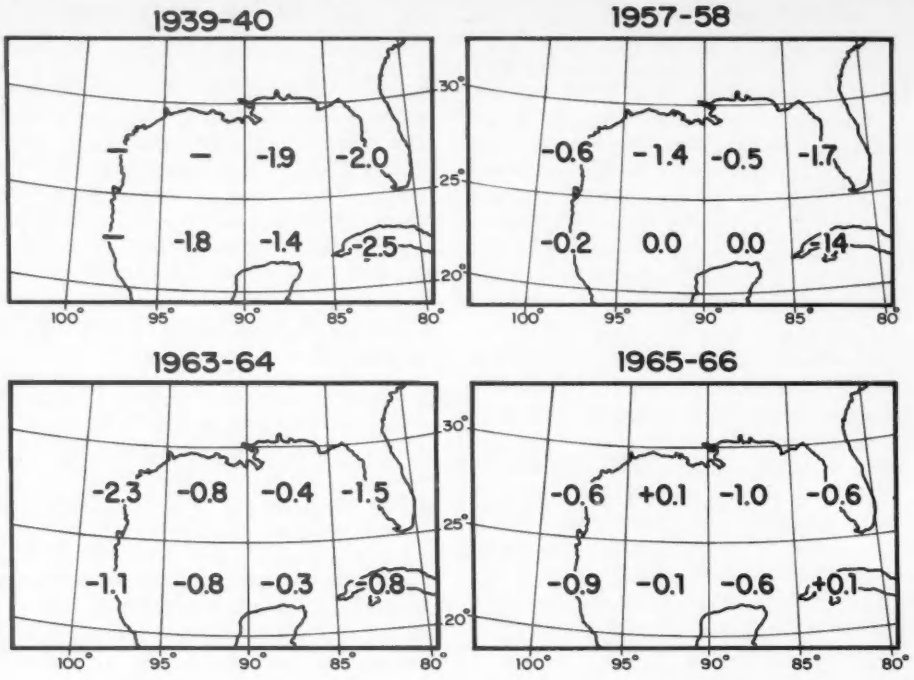

FIGURE 5.—Sea-surface temperature anomalies (°C) in the Gulf of Mexico for selected winters.

During the recent 1972-73 El Niño, however, a situation occurred where this relation did not exist. A trough did not develop off the eastern seaboard until late winter and was short-lived in nature. During most of the winter it was situated over the central United States. Consequently, the flow of cold, continental air over the Gulf of Mexico, especially in the eastern Gulf, was not as intense as in previous El Niño years, and thus not as much cooling of surface waters occurred in the Gulf of Mexico.

A situation opposite to the cold winters along the eastern seaboard described above occurred in the winter 1948-49. Very little cooling occurred in the waters of the Gulf, and the net heat exchange at the air-sea interface likewise was small (Figure 4). The sea-surface temperature anomaly patterns in the winter of 1948-49 compared to the winter 1957-58 are remarkably opposite in sign and magnitude (Figure 6). Whereas, cold sea temperature anomalies prevailed in the latter winter off the southeastern United States, widespread warm anomalies were present in the winter 1948-49. In this winter a distinct ridge developed over the eastern United States in the 700-mb heights, a trough over the western U.S., and another ridge in the northeast Pacific (Figure 7) which is consistent with the hypothesis given by Quinn (1972) and by the findings of Namias.

Namias (1972) suggested that the 1957-58 winter marked the beginning of a new climatic regime in the northern hemisphere. He shows, for example, that the winter mean air temperature at Atlanta, Ga. for the decade 1948-57 was about 5°F higher than the following decade. A trend is also noted in decadal differences of sea temperatures in the Gulf of Mexico. The 1948-57 decade average of February sea temperature was about 1.0°C higher than the 1958-67 February average. Somewhat lower sea temperatures generally prevailed along the entire eastern seaboard in the 1958-67 decade compared to the one preceding.

Sea temperatures and circulation off the U.S. west coast also showed a climatic change. Huang (1972) calculated that southward transport in the general area of the California Current from San Diego to long. 150°W in the period 1958-69 was less than in the previous decade. He showed further that the California Current annual sea temperatures were as much as 1.4°C above normal in the

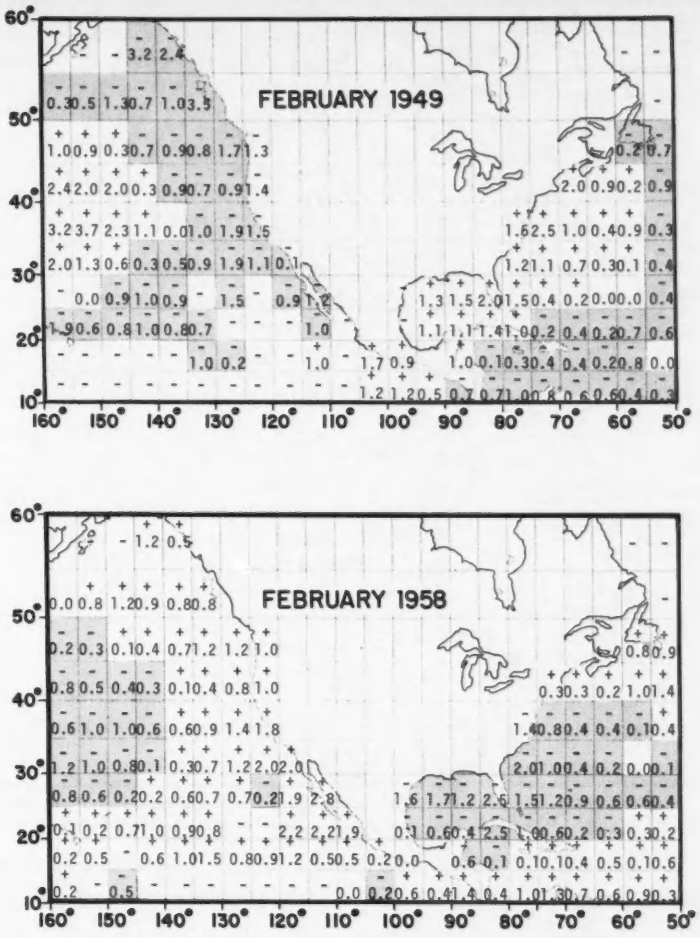

FIGURE 6.—Sea-surface temperature anomalies (°C) February 1949 and February 1958 in eastern Pacific and western Atlantic oceans. Shaded areas colder than 20-yr (1948-67) mean.

1958-69 period and the seasonal temperature departure in winter was greater than 2°C in some places. Apparently, this was caused by less advection of cold subarctic water southward.

DISCUSSION

The authors have attempted to show that development of sea-surface temperature anomalies in the Gulf of Mexico and along the U.S. eastern seaboard in wintertime may be related to the origin of the overlying air masses. In situations where trough development occurs in the upper air circulation over the eastern United States, cold continental air from North America is likely to flow over the Gulf and waters off the eastern seaboard causing excessive loss of heat through evaporation and conduction of sensible heat. Conversely, in situations where a ridge develops, warm air masses predominate, and loss of heat from the ocean is retarded. In fact, as Figure 4 indicates, the water in some winters may cool very little. Furthermore, an attempt has been made to show that the development of these

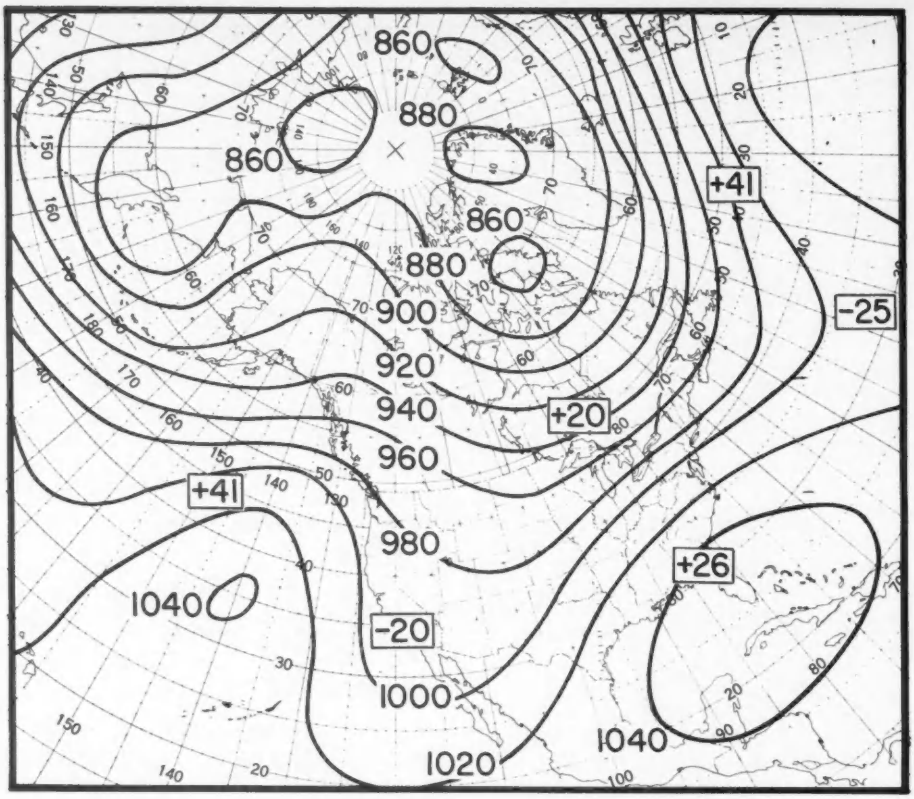

FIGURE 7.—700-mb heights and departures from normal, tens of feet, January 1949. Major departures are enclosed in boxes.

troughs and ridges in the upper air circulation may have been related to air-sea interaction processes in the Pacific Ocean.

It is interesting to speculate on the physical consequences following the development of a large-scale cold sea-surface temperature anomaly in the winter of 1957-58 in the Gulf of Mexico and western Atlantic. It is quite possible that further investigation will show differences of flow in the Gulf Stream. The fact that the anomaly developed in winter suggests that the water to the depth of the thermocline may be affected. A large cold mass of water of this type alters the density distribution over a large area and thus alters the surface circulation. The authors have noted an apparent drift of the anomaly away from the U.S. east coast northeastward until the early summer of 1958 when the surface anomalies were obscured, although it may be quite possible and even likely that the deeper waters were still colder than usual. The effects on Europe of this cold water mass after a period of eastward drift can only be speculated at this time. The fact that the anomaly could be traced for a time following its formation suggests an interesting possibility for further research.

The biological consequences of such large-scale air-sea interactions are even more complex. The effect of the warm sea temperature pool in the eastern Pacific in 1957 and 1958 on fish populations is well documented by Radovich (1961). Southern species were found much farther north than normal in the temperate northeastern Pacific apparently in response to the warm sea temperatures. In the western Atlantic and Gulf the effects of the cold anomaly were less evident although there is a suggestion from the work of Williams (1969) that the shrimp populations were affected.

Williams believes that catches of penaeid shrimp in the southeastern United States fluctuate in such a way as to suggest dependence on coastal temperatures. His studies show an apparent association of good catches with warm years and poor catches with cold years. The shrimp season following the cold winter of 1957-58 was particularly poor in several areas. His indices of cold and warm years are derived from coastal air temperatures which probably are a reasonable indicator of sea temperature variation in estuarine and coastal waters. Williams believes it might be possible to use winter coastal air temperatures as predictors for the succeeding year's catch when better definition and measure of fishing effort are available.

These hints of biological consequences of large-scale air-sea interactions point out possibilities for future research. Clearly, investigations of this nature will require a cooperative effort among meteorologists, oceanographers, and fishery biologists.

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GEOGRAPHIC AND HYDROGRAPHIC DISTRIBUTION OF ATLANTIC MENHADEN EGGS AND LARVAE ALONG THE MIDDLE ATLANTIC COAST FROM RV *DOLPHIN* CRUISES, 1965-66

ARTHUR W. KENDALL, JR.[1] AND JOHN W. REINTJES[2]

ABSTRACT

Atlantic menhaden, *Brevoortia tyrannus*, eggs and larvae were collected during eight ichthyoplankton cruises of the RV *Dolphin* from December 1965 to December 1966. On each cruise tows were made with a Gulf V plankton net at 92 stations along 14 transects from the coast to the edge of the continental shelf from Martha's Vineyard, Mass., to Cape Lookout, N.C. Larvae resulting from a protracted spawning season were taken throughout the year. Eggs were taken over the middle of the shelf in fall. Seasonal shifts in geographic pattern of larvae indicated spawning started in summer off New Jersey and New York, became widespread in the Middle Atlantic Bight in fall, and continued into winter off North Carolina. Larvae were equally distributed in shallow (0-15 m) and deep (18-33 m) tows during night and day. Larvae occurred over a water temperature range from 0° to 25°C and a salinity range of 29 to 36‰. Seasonal distribution of larvae suggests some of the annual variation in year classes may be due to cold-related mortality of larvae entering middle Atlantic estuaries in late fall.

Along the Atlantic coast spawning and early development of many fishes occur in the ocean. The distribution of early stages of most coastal species is inadequately known. Personnel of the Sandy Hook Marine Laboratory designed a program to determine the spawning times and localities of migratory coastal fishes through a series of cruises off the Atlantic coast from Martha's Vineyard, Mass., to Cape Lookout, N.C. From December 1965 to December 1966 eight survey cruises were conducted to collect fish eggs, larvae, and juveniles. These cruises, together with data on juvenile and adult distribution, provided information on the oceanic life history of most of the commercial and sport fishes of the region.

Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), an important commercial and forage fish, was among the species collected during this survey. The early life history of menhaden has puzzled scientists since early accounts by Baird (1873) and Goode (1879). The eggs and larvae were first described by Kuntz and Radcliffe (1917). After early development at sea, the larvae enter estuaries along the coast where they metamorphose into juveniles. June and Chamberlin (1959) concisely review the estuarine stage of menhaden.

The seasonal cycle of menhaden spawning has been inferred from ovary studies by Higham and Nicholson (1964). From Maine to eastern Long Island ovarian development starts in May and reaches a peak in October. The seasonal occurrence of sexually mature fish begins in New Jersey and Delaware in April, continues sporadically in summer, and reaches a peak in October. Around Cape Hatteras maturing fish were taken mainly in late fall; some are found as late as March.

Atlantic menhaden eggs and larvae have been collected offshore and in estuarine waters along the Atlantic coast (Table 1). These collections show a pattern similar to that found by Higham and Nicholson (1964). Spawning off New England occurs in late spring and early summer and again in early fall. Off the middle Atlantic coast eggs and larvae are found in late fall and in spring. Off North Carolina young occur in winter and spring.

Inlet and estuarine studies have collected larval menhaden as they emigrate from the ocean (Table 1). The time of entry varies considerably along the coast and from year to year in the same estuarine areas. In some years entry occurs in late fall, before lowest temperatures are reached. In other years entry occurs primarily as temperatures are warming in early spring. Larvae in the estuaries are apparently killed if winter temperatures fall below 3°C (Reintjes and Pacheco 1966). Emigration from the estuaries varies from late August in the north to January in the south, with some

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TABLE 1.—Collections of menhaden eggs and larvae, east coast of United States.

Reference	Sampling period: Years	Sampling period: Months	Sampling area	Occurrences
Open ocean				
Marak and Colton 1961	1953	Mar.-June	Georges Bank-Gulf of Maine	June—1 egg, off Martha's Vineyard
Marak, Colton, and Foster 1962	1955	Feb.-May	Georges Bank-Gulf of Maine	May—eggs, 130 km off Nantucket
Marak, Colton, Foster, and Miller 1962	1956	Feb.-June	Georges Bank-Gulf of Maine	June—larvae, off Woods Hole
Reintjes 1961	1953-54	all	Cape Hatteras-Florida	Dec.-Feb.—eggs Dec.-Mar.—larvae, off North Carolina
Massmann et al. 1962	1959-60	all	Off Chesapeake Bay	Nov.-Apr.—larvae
Reintjes 1969	1966	Dec.	Off North Carolina	Dec.—eggs, patch of several thousands
Bays and open sounds				
Bigelow and Schroeder 1953			Gulf of Maine	Oct. 1900—young fry, Casco Bay
Kuntz and Radcliffe 1917			Near Woods Hole, Mass.	Oct. 1915—eggs and larvae, Nantucket Sound Aug.—eggs, off Gay Head July—larvae, Woods Hole Harbor
Hildebrand and Schroeder 1928	1912-22		Chesapeake Bay	Jan.-May—large larvae
Pearson 1941	1929	May-Oct.	Lower Chesapeake Bay	May—larvae
	1930	Apr.-Dec.	Lower Chesapeake Bay	Apr.—larvae
	1931	Jan.-Mar.	Lower Chesapeake Bay	
Perlmutter 1939	1938	May-Oct.	Around Long Island	May-Oct.—eggs May-Sept.—larvae
Merriman and Sclar 1952	1943-46	all	Block Island Sound	Fall—larvae (see Wheatland 1956)
Wheatland 1956	1952-53	all	Long Island Sound	June-Oct.—eggs June and Sept.-Dec.—larvae
Richards 1959	1954-55	all	Long Island Sound	May-Oct.—eggs June-July and Sept.-Dec.—larvae
Deubler 1958	1955-57	Dec.-Apr.	Bogue Sound, N.C.	Winter and spring—larvae, common
Herman 1963	1957-58	all	Narragansett Bay	May-Aug. and Oct.—eggs June, July and Oct.-Feb. (most in Oct.)—larvae
Croker 1965	1960-61	all	Near Sandy Hook, N.J.	May-June—eggs Nov.-Dec.—larvae
Dovel 1971	1963-67	all	Chesapeake Bay	Spring and summer near Solomons, Md.—eggs Mar.-June and Nov.—larvae, upper Chesapeake Bay
Inlets				
Reintjes and Pacheco 1966	1955-61	Sept.-June	Indian River Inlet, Del.[1]	Oct.-May—larvae, month of peak occurrence varied with year from Dec.-Feb.
de Sylva et al. 1962	1956-58	all	Indian River Inlet, Del.[1]	Nov.-May—larvae
Tagatz and Dudley 1961	1957-60	all	Beaufort Inlet, N.C.	Jan. and Apr.-May—larvae
Lunz 1965	1964	Jan.-Mar.	Several South Carolina inlets	Feb.-Mar.—larvae
Lewis and Mann 1971	1966-68	Nov.-Apr.	Bogue and Beaufort inlets, N.C.	Nov.-Apr.—larvae
Smaller estuaries				
Warfel and Merriman 1944	1942-43	all	Morris Cove, Conn.	July-Nov.—larvae
Massmann et al. 1954	1950-52	Mar.-Oct.	Five Virginia tidal rivers	Apr.-May—larvae, brackish water
Pacheco and Grant 1965 Reintjes and Pacheco 1966	1955-61	Sept.-June	White Creek, Indian River, Del.	Nov.-June, most Feb.-June—larvae
Tagatz and Dudley 1961	1957-60	all	Neuse River, N.C.	Jan.-June and Sept.-larvae
Pearcy and Richards 1962	1959-60	all	Mystic River, Conn.	June-July—larvae
Dovel 1967	1965-66	all	Magothy River, Md.	Mar.—larvae
Wilkens and Lewis 1971	1967-69	all	White Oak River, N.C.	Jan.-Apr.—larvae

[1]Larvae emigrating from ocean.

juveniles overwintering in southern estuaries. Fish range from 50 to 160 mm when they leave the estuaries (June and Chamberlin 1959).

Recently Mansueti and Hardy (1967) amplified the descriptions of young menhaden and Reintjes (1969) reviewed the biology of the species.

This paper describes the occurrences of menhaden eggs and larvae in the *Dolphin* surveys and relates these findings to daylight, temperature, salinity, and depth, and to our understanding of menhaden early life history.

PROCEDURES

The eight ichthyoplankton cruises were made at approximately 6-wk intervals from December 1965 to December 1966 (Clark et al. 1969). On each cruise 92 stations were located along 14 transects from Martha's Vineyard to Cape Lookout (Figure 1). Stations were closely spaced inshore (9.3 km) along the transects and farther apart (27.8 km) offshore. The order that the transects were run and the time during the 24-h workday that stations were occupied varied among the cruises.

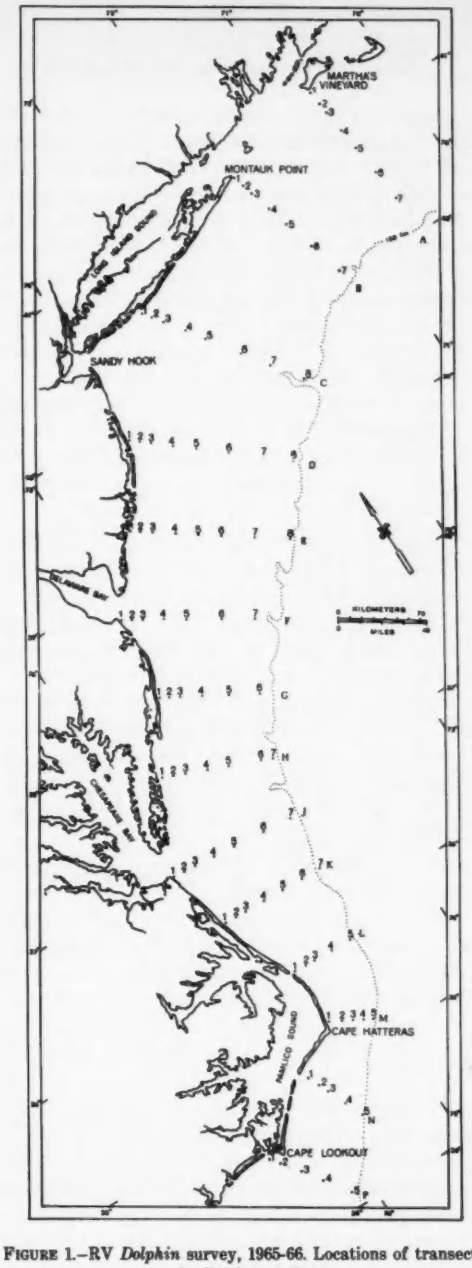


FIGURE 1.–RV *Dolphin* survey, 1965-66. Locations of transects and collecting stations.

Gulf V plankton samplers with 0.4-m openings and 0.52-mm wire mesh were towed for 30 min at 5 knots (2.6 m/s) in step-oblique tows at each station. Two nets were fished simultaneously at six 3-m depth intervals, from separate warps, one shallow (0-15 m) and one deep (18-33 m), where water depth permitted. In shallower water fewer depth intervals were sampled for longer time periods. Plankton samples were preserved in 4% buffered formaldehyde solution and brought to shore for sorting. Supplementary data collected at each station included water temperature and salinity with depth. A scaled-down Cobb midwater trawl was towed at about half of the stations to collect juvenile fishes.

Fish eggs and larvae were separated from the plankton in the laboratory. Clupeoid larvae were distinguished by their slender body, long gut, sparse pigment, and short dorsal and anal fin bases (Table 2), and separated from other larvae.

Several other fishes whose long slender larvae resemble clupeoids occur in the area but they differ in certain features. Lizardfish larvae have a large finfold, an adipose fin later in development, and a row of 6 to 12 paired dark patches ventrally along the body (Anderson et al. 1966). Other elongate salmoniform larvae generally have an adipose fin, photophores often, and oval or stalked eyes. Sand lance larvae have little pigment, but the dorsal and anal fins extend most of the length of the body (Norcross et al. 1961). Blennioid larvae have a short gut, with the anus forward of midlength of the body, and long dorsal and anal fin bases. Other larvae are excluded by myomere counts which fall outside the range for clupeoids (38-55) or by other distinctive characters not found on clupeoid larvae.

TABLE 2.–Distinguishing features of Atlantic coast clupeoid larvae.

Character	Distinguishing features
Body shape	Body slender and elongate, the greatest body depth less than 20% of total length. Anus in posterior third of body.
Fin positions	Dorsal – single, short, about two-thirds way back along body; no adipose fin. Anal – posterior to at least part of dorsal fin, not confluent with caudal fin. Pelvics – abdominal, at about midlength on the body.
Meristic counts	Myomeres (vertebrae) – 38-55. Dorsal fin rays – 9-22. Anal fin rays – 10-30. Principal caudal fin rays – 10 + 9.
Pigmentation	Little pigment except ventrally. Ventral pigment – small spots on throat, along the gut, and at base of caudal fin.
General	Eyes round, in orbits, not stalked. Gut straight with annular folding of the intestine.

Identification of menhaden eggs and larvae among the four other clupeid genera and two engraulid genera along the North American east coast was facilitated by published illustrations and descriptions (Kuntz and Radcliffe 1917; Mansueti and Hardy 1967; Houde and Fore 1973) and reported spawning areas and times (Reintjes 1961; Higham and Nicholson 1964). Menhaden larvae collected north of Cape Lookout are presumed to be *Brevoortia tyrannus*, since *B. smithi* occurs mainly farther south and spawns inshore (Reintjes 1962). The areas of larval occurrence of menhaden overlap Atlantic herring, *Clupea harengus harengus*, in the north, and round herring, *Etrumeus teres;* Spanish sardine, *Sardinella anchovia;* and Atlantic thread herring, *Opisthonema oglinum*, in the south.

Clupeoid larvae less than 8 mm are difficult to distinguish because the median fins and other characters are not formed. However, pigmentation, body shape, and gut length are helpful in small larvae. Among clupeoid larvae the stage of development at a particular size and area of capture are helpful. For each comparable stage of larval development, menhaden are larger than anchovies, Spanish sardine, and Atlantic thread herring, and smaller than Atlantic herring. Only round herring show the same development with size as menhaden but are easily distinguished by the relative length of the snout at all sizes.

Menhaden were counted and total length measurements of larvae less than 12 mm long were made to the nearest 0.1 mm with an ocular micrometer in a dissecting microscope; those longer than 12 mm were measured with dividers and a steel rule or dial calipers to the nearest 0.5 mm. Samples containing more than 50 fish were usually randomly subsampled before measuring. To get a subsample of 25-50 larvae, the sample was floated in formaldehyde solution in a 150-mm petri dish scribed into quarters with two diameters; a random half or quarter of the dish was chosen for measuring. The process was repeated with the chosen fraction with samples of more than 200 specimens. When larvae showed slight damage, such as broken caudal rays, measurements were adjusted to approximate total length. Larvae identifiable, but too mutilated to be measured, were counted. For geographic distribution analysis, numbers of larvae at each station were adjusted to a standard tow as in Smith (1973) and Fahay (1974).

RESULTS

Geographic Distribution of Larvae

Menhaden larvae are more widely distributed than any other clupeoid in the northwest Atlantic. Larvae have been reported from Maine to Mexico in oceanic, estuarine, and fresh waters. South of Cape Hatteras Atlantic menhaden spawn in the cooler months (October to June), while along the Middle Atlantic states they spawn during the warmer months (June to November). Seasonal occurrences of larvae followed the annual north-south migration of adults. Small larvae were first collected in June near Delaware Bay. By October larvae were present from southern New England to Chesapeake Bay. In late fall they were found from New York to Cape Lookout. During the winter and spring larger larvae were present from Chesapeake Bay to Cape Lookout.

Small menhaden larvae were collected throughout the year except in late spring, indicating nearly continual spawning (Figure 2). Menhaden hatch at about 3 mm (Mansueti and Hardy 1967), but we caught few less than 5 mm. This was probably due in part to our inability to identify with certainty small larvae and in part to their fragile, slender form which caused them to be extruded from our nets. The largest larvae we collected were 30 mm, about the size at which they enter estuaries and transform into juveniles (Lewis et al. 1972).

It is not reasonable to attempt to determine a growth rate for menhaden larvae from our data. Small menhaden less than 8 mm were collected from June through February. Thus, spawning took place in our sampling area for 6 mo of the year. This protracted spawning season and probable geographic movements of larvae preclude the possibility of determining growth rate from this survey.

Data associated with collections of menhaden larvae are presented in the Appendix Table. Their occurrences are illustrated in Figures 4-11. From the irregular horizontal and vertical distributions and highly nonnormal catch frequency curve (Figure 3), it appears that the larvae are very unevenly and probably patchily distributed. The location and density of patches may be related to local currents and water conditions on a smaller scale than we sampled. This discussion follows the sequence of spawning, i.e. starting in late spring

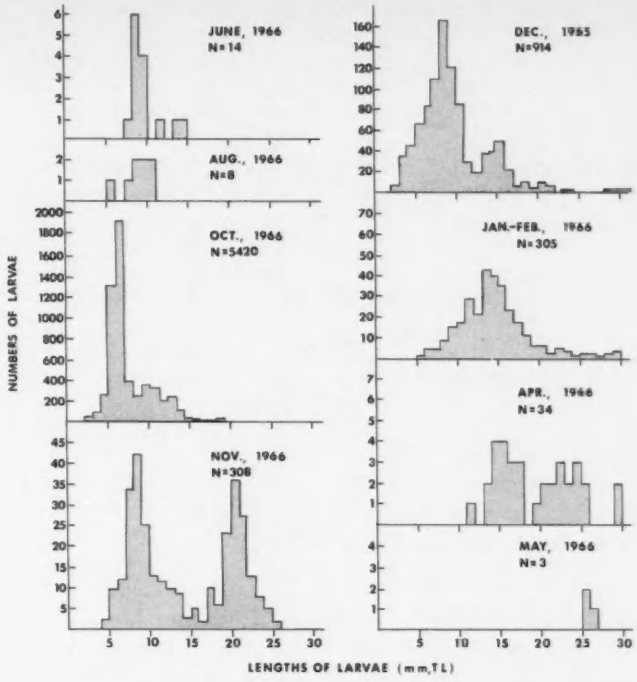


FIGURE 2.–Length-frequencies of menhaden larvae from the RV *Dolphin* survey, 1965-66.

1966. The cruises, however, began in December 1965. Thus, the cruises from December 1965 to May 1966 cover one spawning season and those from June 1966 to November-December 1966 cover the following season.

In late June a few larvae were collected nearshore off Delaware Bay (Figure 4). These larvae were small (7.8-14.4 mm), indicating they had been spawned recently. Spawning may have occurred in Delaware Bay since the larvae we

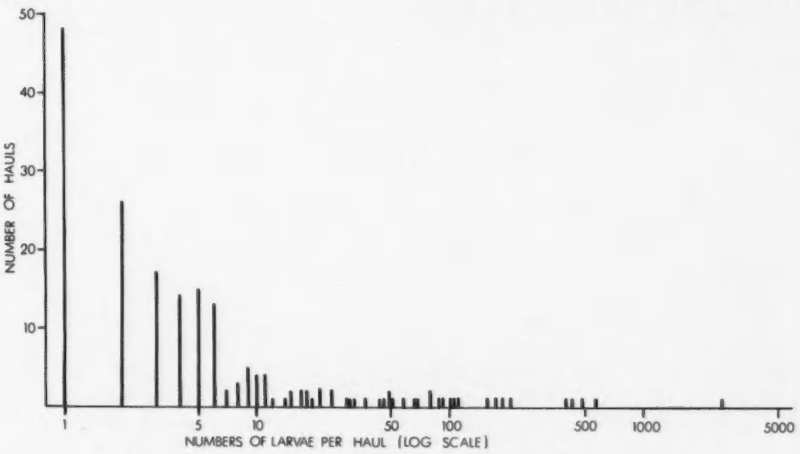


FIGURE 3.–Frequency distribution of menhaden larval catches per haul.

caught were concentrated close to its mouth. The distribution of the collections indicates spawning was not widespread. Stations north of these collections were sampled about 10 days earlier, possibly accounting for the limited distribution we observed. The absence of larvae to the north in these earlier collections would indicate spawning had recently started. Temperatures in June in the area of capture ranged from 15° to 19°C, and salinity varied from 30.3 to 32.1‰ (Figure 4). Hydrographic conditions within these ranges occurred widely along the coast during this cruise (Clark et al. 1969).

During our cruise in August there was evidence of limited spawning nearshore (Figure 5). A few small larvae, 5.6-10.5 mm, were taken off Long Island and New Jersey. Perhaps the earlier spawning in June was so limited that with dispersal during growth, insufficient larvae survived to be taken in our August sampling. Temperatures in the area of capture in August were warmer than in June, 18° to 22°C at the surface, and the seasonal thermocline was well developed about 15 m below the surface (Figure 5). Temperatures below the thermocline were less than 10°C. Larvae were collected only in the shallow net, indicating they were in the warm water above the thermocline. Salinity in the area of capture ranged from 30.1 to 31.0‰.

In October 5,420 larvae were collected that ranged from 3.5 to 18.5 mm (Figure 2). The length-frequency distribution was skewed to the left (mean 7.3 mm; mode 6.5 mm). Larvae were more widespread and in greater concentrations than during any other cruise (Figure 6). They occurred from Martha's Vineyard to Currituck Beach, N.C., and were abundant from Long Island to Maryland, near the middle of the shelf. They occurred nearshore from southern New England to New Jersey and near Chesapeake Bay. The fish

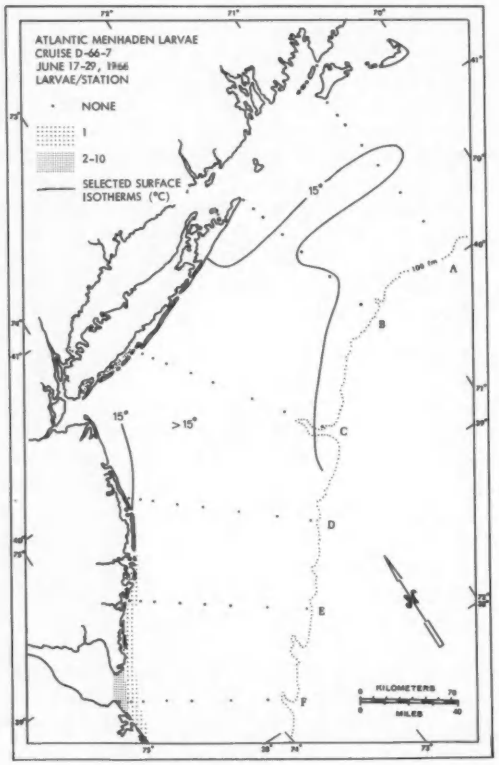


FIGURE 4.—Distribution and abundance of menhaden larvae in the June cruise.

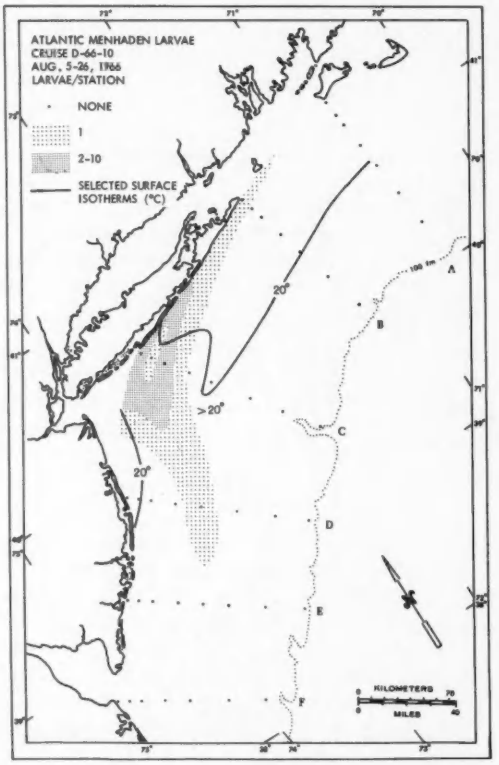
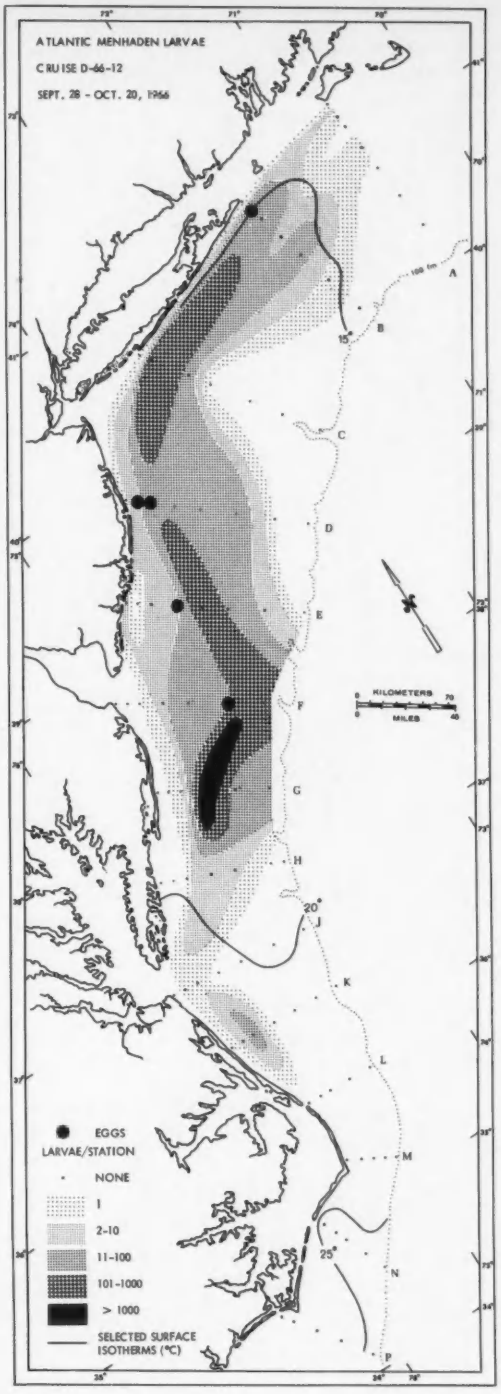


FIGURE 5.—Distribution and abundance of menhaden larvae in the August cruise.



were 8-12 mm in the northern part of the sampling range, from New York north. Fish in a broader size range, 4-12 mm, were present off New Jersey. Nearly all fish south of New Jersey were smaller, 4-8 mm.

In October the thermocline was breaking down but still present over much of the area, and surface temperatures were about 3°C cooler than in August (Figure 6). Salinity values were about the same as in August, mostly between 30.5 and 32.0‰, except near the mouth of Chesapeake Bay where they dropped to 28.0‰.

The cruise in late fall 1966 (Figure 7) shows a distribution pattern quite similar to the cruise in December 1965 (Figure 8). During both cruises, larvae occurred mostly nearshore from Long Island to North Carolina. They were most abundant near Cape Hatteras, where they were taken to the edge of the shelf.

In November 1966 there was a bimodal size distribution with one peak at 8 mm and the other at 20 mm (Figure 2). There were few larvae between 14 and 18 mm. In December 1965 the peak at 8 mm is similar to that in late fall 1966, but the second peak at 20 mm is not seen (Figure 2). Possibly this difference is due to year-to-year variation in spawning pattern in the area studied.

In the November and December cruises, small fish were found south of Delaware Bay and tended to occur at least 12 km offshore. Larger fish occurred mainly north of Chesapeake Bay and mostly within 15 km of shore. In transition areas between north and south and inshore and offshore areas, fish in a wide length range occurred at the same station and bimodal length-frequency curves were seen. This may indicate that spawning occurs in waves, and as the larvae grow they disperse from the area where they were spawned.

By late fall the thermocline was gone and surface isotherms roughly paralleled the coastline (Figures 7, 8). Larvae were taken over a wide range of temperature, from 7° to 25°C. Most collections were in water between 10° and 20°C. Salinity varied considerably between the two late fall cruises. In 1965, several patches of low saline water, less than 30‰, were found mostly near the shore (Clark et al. 1969). However, in 1966 salinity throughout the area was greater than 31‰, except immediately outside Chesapeake Bay. The distribution of larvae is quite similar between these

FIGURE 6.—Distribution and abundance of menhaden larvae and distribution of menhaden eggs in the October cruise.

two cruises in spite of these differences in salinity.

In February menhaden larvae were taken from Virginia to Cape Lookout (Figure 9). They probably occurred farther south than we sampled since they were most abundant on our southernmost transect. Most larvae were taken between Cape Hatteras and Cape Lookout. Lengths presented a fairly symmetrical distribution with a peak at 13 mm (Figure 2). There is indication again that the larger fish were taken nearer to shore and farther north than the smaller fish. Few fish shorter than 8 mm were seen at this time, and the maximum length was 29 mm. Apparently, at about this size menhaden have either entered estuaries or can avoid our nets. In winter the temperature was 4°C at 11 of the 23 stations where menhaden were taken; it was less than 3°C at 4 stations (Figure 9). Water at these stations was practically isothermal with depth (Clark et al. 1969).

During April larvae occurred in approximately the same areas as in February (Figure 10). Fewer, larger larvae were taken between Chesapeake Bay and Ocracoke Inlet, N.C., than earlier. Larvae north of Cape Hatteras ranged from 21 to 29 mm. Off Ocracoke Inlet larvae were 11-19 mm. The larger larvae north of Cape Hatteras were taken nearshore; those farther south extended 37 km offshore. A bimodal length-frequency curve had peaks centered at 15 and 24 mm, although insufficient numbers of fish were collected to determine the statistical significance (Figure 2). By April, temperatures in the areas of capture were warmer than winter temperatures, above 8°C, and mostly between 10° and 12° (Figure 10). Salinity ranged from 30.3 to 35.6‰.

In May a few large (25-26 mm) larvae were taken off Virginia, inshore near Chesapeake Bay (Figure 11). These were apparently remnants of the early winter spawning, the rest of the larvae having already entered estuaries. Water in the areas of capture had warmed to 13° to 17°C (Figure 11). Salinity was generally lower, from 28.4 to 31.2‰, due to spring freshening nearshore (Clark et al. 1969).

Temperature-Salinity Relations

The catches of menhaden larvae during all cruises in the shallow net were compared

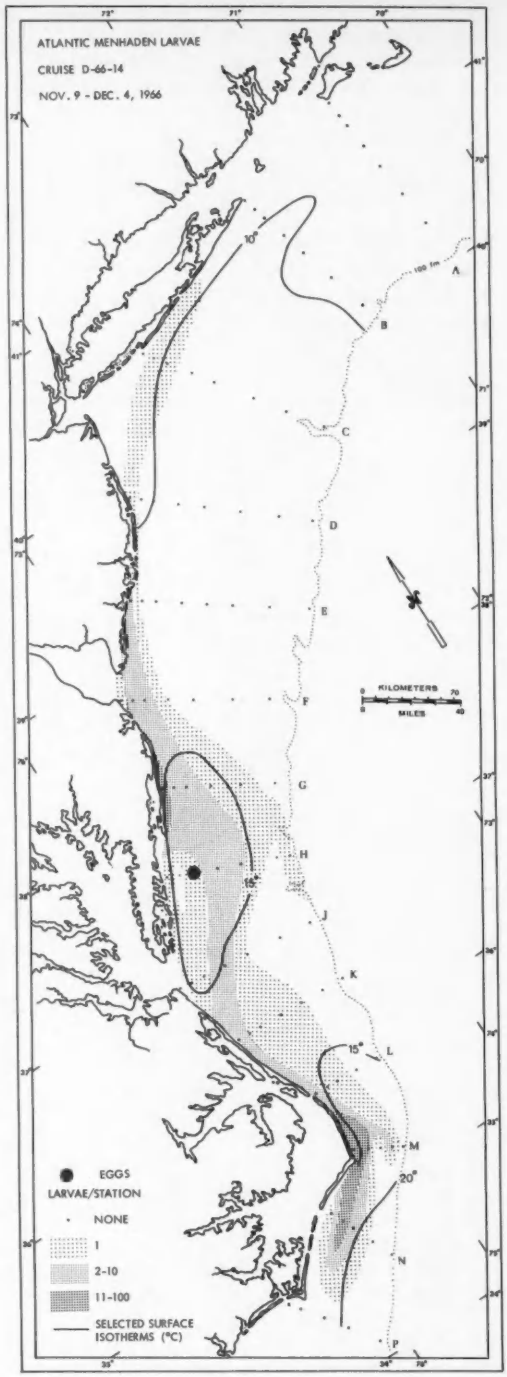
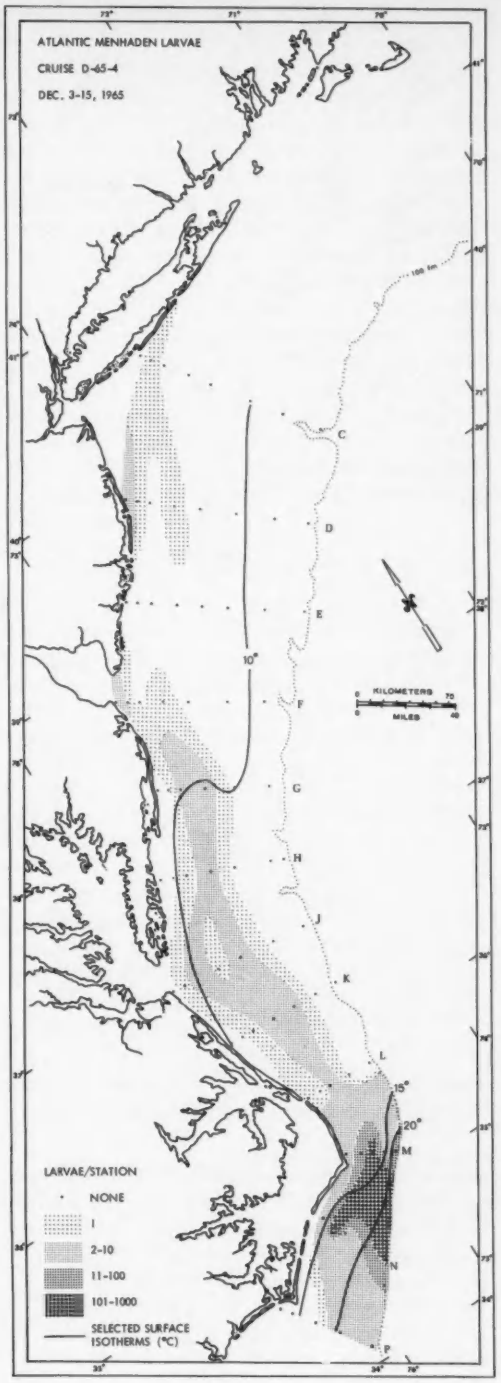


FIGURE 7.—Distribution and abundance of menhaden larvae and distribution of menhaden eggs in the November-December 1966 cruise.



graphically with observed surface temperatures and salinities. Surface observations were thought adequate since most larvae were collected when hydrographic conditions were nearly uniform with depth and menhaden larvae were scarce below the thermocline. Mean temperatures and salinities within the sampling depth range were also compared with catches and showed patterns similar to those discussed here.

Observed surface temperatures varied from -1° to 28°C (Figure 12). At each of nine whole-degree intervals between 6° and 19°C, more than 30 stations were occupied. More than 40 stations were occupied at 10° and 14°C. Menhaden occurred at stations when temperatures were between 0° and 25°C. The curve of positive stations (those where menhaden were taken) was similar in shape and range to that of total stations. The numbers of larvae taken at each temperature were plotted on a log scale. This plot was slightly skewed to the right, with modal catch at 18°C. Catches of over 100 larvae were made at temperatures from 9.3° to 20.5°C, with most between 15.8° and 18.5°C.

Surface salinity varied from 23 to 38‰, with a mode at 31‰ (Figure 13). Positive stations occurred over the entire range of salinities, with a mode at 30‰. The larval catch curve, on a log scale, is similar in shape to the total station curve, with a mode at 31‰. At stations with salinities between 30 and 36‰, a total of at least 200 larvae were taken within each part-per-thousand interval.

Diel-Vertical Comparisons of Larval Catches

Comparisons were made of the catches of larvae in shallow and deep tows made during night and day. These comparisons are on the basis of the volume of water sampled, which was assumed to be constant among the tows. The use of parametric statistics was precluded by the highly nonnormal catch frequency curve (Figure 3). Of the 172 tows with menhaden larvae, 48 contained only 1 larva, and 11 tows contained more than 100 larvae. Of the 11 tows with more than 100 larvae, 7 were taken in shallow tows during daylight. Altogether menhaden occurred in 85 daylight tows and 87 nighttime tows (Table 3). The distribution of catches was not significantly different with time of day (chi-square test; $P > 0.50$). Day and night

FIGURE 8.—Distribution and abundance of menhaden larvae in the December 1965 cruise.

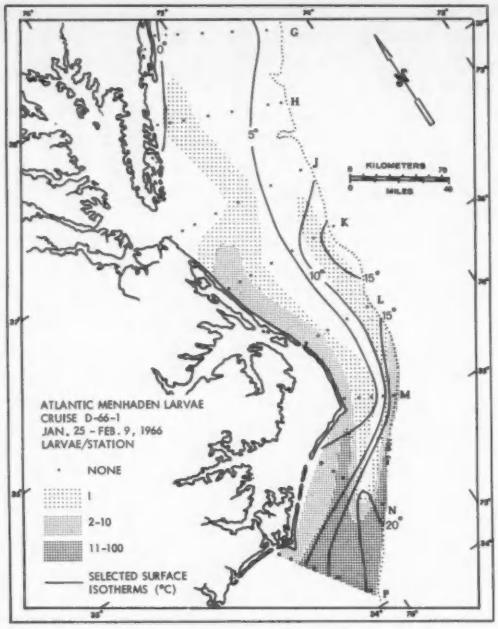


FIGURE 9.—Distribution and abundance of menhaden larvae in the February cruise.

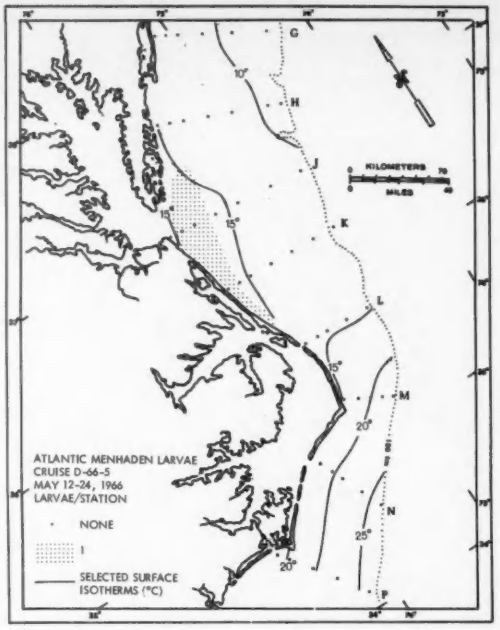


FIGURE 11.—Distribution and abundance of menhaden larvae in the May cruise.

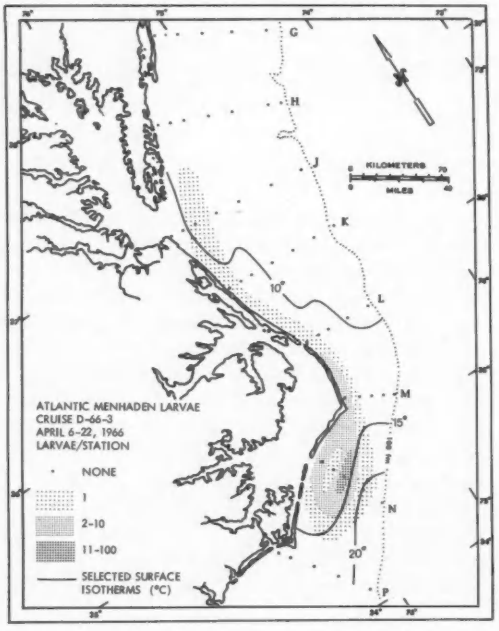


FIGURE 10.—Distribution and abundance of menhaden larvae in the April cruise.

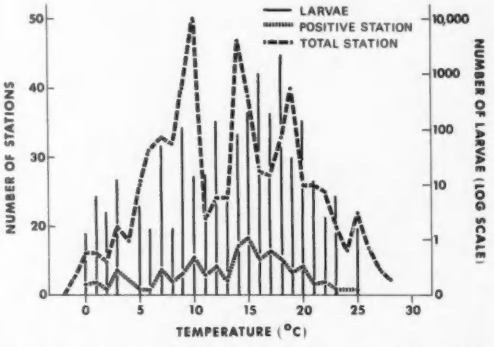


FIGURE 12.—Relation between surface temperature to menhaden larval catch and sampling effort.

tows were combined to compare the distribution of catches by the shallow and deep nets. By the shallow net, menhaden were taken in 138 tows and by the deep net in 34 tows (Table 3). The distribution of catches was not significantly different in the two nets ($P > 0.50$). Comparisons of size of larvae between day and night tows with the shallow and deep nets showed no significant differences.

Eggs

We found menhaden eggs at only six stations, five from the October cruise and one from the late fall cruise in 1966 (Figures 6, 7). All but one sample contained less than 100 developing eggs. The exceptional sample was from 85 km off Delaware Bay in October where about 2,000 eggs were taken. Precise counts were not possible due to the poor state of preservation of the samples when they were examined. Eggs were collected in areas where small larvae were taken. Apparently menhaden spawn as large schools producing dense patches of eggs (Reintjes 1969). During the short incubation time (48 h), these patches do not become dispersed. Thus the distribution of menhaden eggs at sea is probably more uneven than that of larvae. Chance was a dominant factor in catching menhaden eggs so distributed in our survey.

Mid-Water Trawl Catches

Sampling by mid-water trawl during the cruises collected a few larval and adult menhaden. Sampling effort was good in areas where the catches were made, so they probably reflect the actual geographic distribution of menhaden subject to capture by this type of sampling (Clark et al. 1969). A few large larvae, 21-37 mm, were taken in August off the Chesapeake Bay area. Age-0 fish, 89-177 mm FL (fork length) (Reintjes 1969), occurred close to shore from southern New England to Chesapeake Bay in late fall 1966. These probably represent young fish migrating south after spending the summer in estuaries (June and Chamberlin 1959). Other catches included two large fish, 305 and 361 mm FL, close to shore off southern New Jersey in May, and several age-0 fish off Oregon Inlet, N.C., in June.

DISCUSSION

Much speculation has surrounded the distribution of early stages of menhaden. Spawning times and places have been inferred from examination of gonads of adults (McHugh et al. 1959; Higham and Nicholson 1964) and nearshore and estuarine samples of larvae and juveniles (e.g. Richards 1959; Sutherland 1963; Pacheco and Grant 1965). Few studies have actually taken menhaden eggs and larvae to determine more directly the area of spawning (Reintjes 1961; Massmann et al. 1962). Controversy has concerned whether menhaden spawn in Chesapeake Bay (Hildebrand and Schroeder 1928) and whether there are two separate populations along the east coast, one spawning in spring and one in fall (Nicholson 1972). Annual variation in time of spawning and entry of larvae into estuaries may account for some of the confusion, since most studies have been short-termed and in a relatively small portion of the range of menhaden.

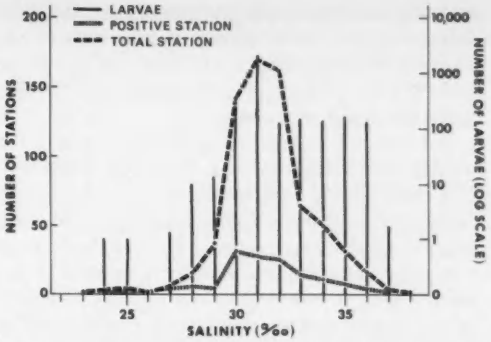


FIGURE 13.—Relation between surface salinity to menhaden larval catch and sampling effort.

Caution needs to be exercised in analyzing the present data since they were collected during a single year and do not encompass the entire range of spawning of menhaden (Reintjes 1969). During summer larvae were taken from our inshore stations to our farthest offshore station and at our most northerly station. The possibility of spawning within estuaries is indicated by the presence of

TABLE 3.—Diel and depth distribution of menhaden larval catches and mean lengths.

Larvae/tow	Day			Night			Day and Night		
	Shallow	Deep	Both	Shallow	Deep	Both	Shallow	Deep	All
	Number of tows								
1-2	29	9	38	34	2	36	63	11	74
3-4	7	3	10	7	4	11	14	7	21
5-20	18	3	21	18	6	24	36	9	45
>21	15	1	16	10	6	16	25	7	32
Total tows	69	16	85	69	18	87	138	34	172
Mean larvae/tow	68.2	6.4	56.0	19.1	48.2	25.6	43.0	27.2	39.8
Mean larval length (mm)	8.3	8.8	8.3	9.0	6.9	8.2	8.5	7.1	8.3

small larvae near their mouths. In winter they were found at our southernmost stations. Therefore, spawning could have taken place inshore and offshore of our stations and farther north and south of our sampling.

Our results on area of spawning confirm the conclusions of Higham and Nicholson (1964) and Nicholson (1972) that menhaden spawn during both their northward spring migration and their southward fall migration. We conclude that spawning apparently continues in winter in the south, based on our catches around Cape Lookout. Midsummer spawning may have occurred north of our sampling area, or may have been inhibited in 1966 by water cooler than usual.

Harrison et al. (1967) postulated that bottom drift of waters off Chesapeake Bay influence the success of year classes of menhaden. During years when bottom drift was weak and southwesterly, poor year classes occurred. However, our data and that of Massmann et al. (1962) do not indicate a preference for bottom waters by larger menhaden larvae. Larvae entering the estuaries are found throughout the water column (Lewis and Mann 1971), and later, in the estuaries, they are found primarily in surface waters (Massmann et al. 1954). Possibly the factors affecting bottom drift also affect the success of year classes, but in an indirect way.

Reintjes and Pacheco (1966) reported on inlet and nursery area collections in Indian River, Del., made over a 6-yr period (1955-61). Among the years studied, the peak in larval abundance at the inlet occurred in all months from December through March. Larvae were taken at the inlet from September through June in most years. It appeared that when temperatures at the inlet dropped to 3°C, larvae in the area were killed. In four seasons, when large catches of larvae were made at the inlet between December and February and temperature later dropped below 3°C, larvae were scarce or absent in upstream nursery areas. However, larvae taken in years when temperature remained above 3°C and those taken after the critical low temperature period were later represented in collections upstream.

Due to the extreme year-to-year variability in time of entry at the inlet at Indian River, it is difficult to relate our catches to these data. The few small larvae taken near Delaware Bay in June would probably have entered the estuary in July, a month when Reintjes and Pacheco (1966) reported none. We made large catches in this area in October. Larvae were also present offshore in November and December. In February, larvae were not taken north of Virginia and water temperature close to shore between Chesapeake and Delaware bays was less than 0°C. From these data, it would appear that 1965-66 was dissimilar to any year studied by Reintjes and Pacheco (1966) with regard to menhaden larvae near Delaware Bay. Presumably during 1965-66 larvae could have been taken in abundance in late fall but would have been killed by cold water in February. Subsequently no larvae would have entered in winter or spring, but some might have appeared in early summer.

Menhaden larvae were taken off Chesapeake Bay in waters 1° to 15°C by Massmann et al. (1962). Herman (1963) reported them in Narragansett Bay from 1° to 22°C. The larvae we collected at temperatures below 3°C did not appear decomposed as would be expected had they been dead when captured. Lewis (1965, 1966) has studied the effects of subjecting menhaden larvae to low temperatures and a range of salinities in the laboratory. He has shown that moderate salinities (10-20‰) enhance survival at low temperature as do lowered acclimation temperatures. At 7°C acclimation temperature, the lowest he used, and 2° to 4°C test temperatures, 50% mortality occurred in about 40 h at 24‰. Salinities in our areas of capture were 31 to 35‰—higher than those tested by Lewis (1966). If temperatures below 3°C in estuarine waters kill many menhaden (Reintjes and Pacheco 1966), it may be advantageous for larvae to remain in the ocean where temperature changes are more gradual. Menhaden entering estuaries are usually larvae less than 30 mm long, and in the estuary they rapidly transform by 38 mm (Lewis et al. 1972). Reintjes and Pacheco (1966) reported a few transforming specimens (greater than 34 mm) entering Indian River in May. That they are dependent on estuarine conditions for transformation is supported by the absence of transforming specimens and juveniles in our collections.

SUMMARY AND CONCLUSIONS

A total of 7,006 menhaden larvae were collected in 172, 0.5-h Gulf V plankton tows. The larvae were taken on eight cruises along the middle Atlantic coast throughout the year. Eggs were taken in a few tows in the fall. The catch distribution was nonnormal, with 48 tows catching only 1 fish and 1

tow catching 2,553 fish. No differences in larval catches or size were found in shallow and deep tows or during day or night. Small larvae, less than 8 mm, were taken from June through February, indicating a protracted spawning period. However, there was a seasonal shift in area of spawning. In late spring and summer limited spawning was occurring off New Jersey and New York. By early fall spawning was widespread from southern New England to Virginia. By late fall and early winter spawning was limited to areas between Delaware and North Carolina. Larger larvae were taken in the north in late fall and south of Delaware Bay in winter and spring.

Larvae occurred over a wide range of temperature, from 0° to 25°C. Several were taken in waters cooler than the 3°C limit found lethal in laboratory tests and inferred to be limiting in inlet sampling studies. Most larvae were collected at temperatures between 15° and 20°C. There was an inverse relationship between temperature and size of larvae.

Salinity seemed to have little influence on the distribution of larvae. They occurred at practically every salinity encountered and the frequency of salinities closely resembled the frequency of positive tows.

Our findings are similar to recent investigations of early life history of Atlantic menhaden based on inlet sampling of larvae, gonad studies, and scale annulus formation. It appears that spawning and early development at sea take place over a long period in a given coastal area, and the larvae resulting from this spawning may reach the inlets over a long seasonal time. In years with mild winters, successful immigration to estuarine areas may occur before the winter temperature minimum. However, under more severe conditions, when winter temperatures in the estuaries fall below 3°C, successful immigration may occur only as temperatures are increasing in spring because larvae entering estuaries during the fall may not survive the winter. This could account for some of the annual variation in year-class strength of Atlantic menhaden.

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APPENDIX TABLE—RV *Dolphin* 1965-66 ichthyoplankton survey. Data associated with Gulf V catches of Atlantic menhaden larvae.

CRUISE STAT. D65 4	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1965 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE		MEAN
C 2	0-15	1	1	19.7			312	2353	NIGHT	27	8.2	8.2	8.2	8.2	8.3	NONE	-	30.0	30.4	30.2
D 1	0- 6	6	6	18.7	15.4	23.8	512	1458	DAY	11	7.7	7.7	7.7	7.7	7.8	NONE	-	29.0	29.1	29.1
D 2	0- 9	1	1	20.2			512	1557	DAY	18	7.9	8.0	7.9	8.0	7.9	NONE	-	29.0	29.6	29.3
D 4	18-24	1	1	16.9			512	1905	NIGHT	33	8.5	8.5	8.5	8.5	8.5	NONE	-	29.4	29.7	29.5
F 1	0- 9	2	2	30.0	29.4	30.6	512	1707	NIGHT	17	7.2	7.3	7.3	7.3	7.0	NONE	-	28.4	28.6	28.5
F 2	0- 9	1	1	23.3			912	1803	NIGHT	17	7.3	7.4	7.3	7.3	7.4	NONE	-	24.3	24.6	24.5
F 4	0-15	1	1	21.0			1012	0119	NIGHT	20	9.1	9.2	9.2	9.2	9.1	NONE	-	30.1	30.2	30.1
G 3	0- 6	6	6	11.9	10.6	13.7	1012	2302	NIGHT	18	9.8	10.0	9.9	10.0	9.5	NONE	-	30.1	30.4	30.3
G 4	0-15	2	2	12.3	10.2	14.4	1012	2126	NIGHT	29	10.1	10.2	10.2	10.1	10.2	NONE	-	31.8	32.2	32.0
H 3	0- 6	2	2	12.1	10.2	14.0	1112	0812	DAY	23	10.8	10.9	10.9	10.8	10.9	NONE	-	28.3	28.4	28.3
H 4	0-15	2	2	11.8	10.9	12.8	1112	1237	DAY	25	10.7	10.7	10.7	10.7	10.7	NONE	-	28.1	30.0	29.2
J 2	0- 3	1	1	17.4			1212	1900	NIGHT	9	9.8	10.3	10.0	9.8	10.8	NONE	-	30.3	30.8	30.6
J 3	0- 6	5	5	16.5	13.7	18.9	1212	1030	DAY	16	10.0	10.9	10.5	10.0	10.9	NONE	-	30.5	32.1	31.4
J 4	0- 6	1	1	10.1			1212	0902	DAY	17	10.9	11.0	11.0	10.9	11.0	NONE	-	32.8	32.8	32.8
J 5	0-15	2	2	15.7	15.6	15.8	1212	0537	NIGHT	26	10.8	10.9	10.8	10.9	10.8	NONE	-	32.5	34.0	33.1
K 3	0-15	1	1	15.1			1312	0038	NIGHT	25	10.2	10.8	10.3	10.2	10.8	NONE	-	33.3	34.0	33.7
K 4	0-15	7	7	15.3	13.7	19.5	1312	0410	NIGHT	31	11.9	12.0	11.9	12.0	11.9	NONE	-	33.9	34.2	34.0
K 4	18-24	3	3	13.6	11.4	15.0	1312	0410	NIGHT	31	11.9	11.9	11.9	12.0	11.9	NONE	-	34.3	34.5	34.5
K 5	0-15	3	3	14.1	13.4	15.1	1312	0607	NIGHT	35	11.3	11.5	11.3	11.5	11.3	NONE	-	32.5	32.9	32.6
L 1	0- 6	1	1	15.2			1312	1939	NIGHT	18	11.3	11.5	11.4	11.3	11.7	NONE	-	33.8	34.6	34.2
L 3	0-15	1	1	19.3			1312	2152	NIGHT	35	12.1	12.4	12.3	12.4	12.2	NONE	-	34.1	34.2	34.2
L 3	18-24	7	7	12.5	9.1	15.9	1312	2152	NIGHT	35	12.2	12.2	12.2	12.4	12.2	NONE	-	33.9	34.1	34.0
M 1	0- 3	18	18	18.4	12.3	21.3	1412	1838	NIGHT	13	12.4	12.4	12.4	12.4	12.5	NONE	-	34.1	34.4	34.2
M 2	0- 9	79	36	14.2	10.1	19.4	1412	1730	NIGHT	18	12.6	12.7	12.6	12.7	12.6	NONE	-			
M 3	0-15	181	77	10.6	5.1	16.3	1412	1553	DAY	20	12.7	12.8	12.7	12.8	12.7	NONE	-	33.2	34.5	33.6
M 4	0-15	5	5	12.8	9.5	14.2	1412	1445	DAY	26	13.0	13.1	13.1	13.1	12.8	NONE	-	34.1	34.5	34.2
M 4	18-24	1	1	11.9			1412	1445	DAY	26	12.8	13.0	12.9	13.1	12.8	NONE	-	34.2	34.2	34.2
M 5	0-15	57	32	7.5	3.5	10.3	1412	1235	DAY	90	23.1	23.1	23.1	23.1	20.1	NONE	-			
M 5	18-33	4	4	9.7	7.8	11.5	1412	1235	DAY	90	22.5	23.1	22.8	23.1	20.1	NONE	-			
N 1	0- 6	5	5	15.3	12.5	19.0	1512	0005	NIGHT	19	14.3	14.4	14.3	14.4	14.3	NONE	-	34.6	34.8	34.7
N 2	0-15	206	81	6.2	2.9	15.2	1512	0058	NIGHT	24	18.4	18.8	18.5	18.4	19.4	NONE	-	35.1	35.8	35.5
N 3	0-15	10	10	9.2	4.9	11.2	1512	0341	NIGHT	25	17.5	17.5	17.5	17.5	17.8	NONE	-	35.3	36.5	35.8
N 4	0-15	36	32	7.5	4.1	12.7	1512	0520	NIGHT	45	19.1	20.6	20.1	20.6	17.6	NONE	-	36.3	36.8	36.6
N 4	18-33	21	21	9.1	5.0	11.7	1512	0520	NIGHT	45	17.6	18.9	18.2	20.6	17.6	NONE	-	36.1	36.2	36.1
N 5	0-15	172	49	8.2	3.9	11.2	1512	0900	DAY	128	20.5	20.5	20.5	20.5	17.0	NONE	-	36.3	36.3	36.3
N 5	18-33	49	45	9.6	5.3	12.7	1512	0900	DAY	128	19.9	20.4	20.2	20.5	17.0	NONE	-	36.3	36.3	36.3
P 4	0-15	9	8	9.2	7.7	12.0	1512	1630	DUSK	34	22.4	23.2	23.0	23.2	19.3	NONE	-	36.9	37.5	37.1
P 4	18-33	2	2	9.2	8.3	10.1	1512	1630	DUSK	34	19.3	22.3	21.5	23.2	19.3	NONE	-			
P 5	0-15	3	3	9.5	8.7	10.7	1512	1335	DAY	82	25.4	25.4	25.4	25.4	23.5	NONE	-	37.4	37.8	37.6

APPENDIX TABLE—Continued.

CRUISE STAT. D66 1	TOW DEPTH (M)	******** LARVAE ******** NUMBER TOTAL	NUMBER MEAS.	LENGTHS MEAN (MM TL)	LENGTHS RANGE (MM TL)	DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	THERMOCLINE DEPTH (M)	SALINITY (0/00) RANGE		MEAN
H 2	0- 6	2	2	21.1	19.4 22.9	7 2	0200	NIGHT	16	0.5	0.7	0.6	0.5	0.7	NONE	-	31.6	32.0	31.8
H 3	0- 6	1	1	15.5		7 2	0059	NIGHT	22	1.5	1.6	1.6	1.5	1.6	NONE	-	32.2	32.4	32.3
J 5	0-15	1	1	23.5		7 2	1143	DAY	26	3.5	3.6	3.5	3.6	3.5	NONE	-	32.9	33.0	33.0
K 1	0- 6	3	3	16.8	9.5 29.4	8 2	0138	NIGHT	15	1.5	1.6	1.5	1.6	1.5	NONE	-	30.9	31.2	31.1
K 2	0-15	4	4	17.3	13.8 24.3	8 2	0038	NIGHT	25	1.5	1.9	1.6	1.8	2.1	NONE	-	31.2	32.1	31.6
K 3	0-15	1	1	17.0		7 2	2332	NIGHT	22	3.4	3.8	3.5	3.8	3.4	NONE	-	32.6	32.6	32.6
K 6	0-15	1	1	17.9		7 2	1938	NIGHT	50	14.4	14.8	14.7	14.4	13.2	NONE	-	34.9	35.1	35.0
L 1	0- 6	6	6	22.3	17.0 29.1	8 2	0711	DAY	19	2.0	2.4	2.2	2.4	2.0	NONE	-	31.9	31.9	31.9
L 2	0- 6	4	4	19.6	15.9 28.0	8 2	0824	DAY	23	3.3	3.4	3.4	3.3	3.4	NONE	-	32.4	32.4	32.4
L 5	18-33	1	1	17.0		8 2	1225	DAY	145	12.2	13.2	12.7	14.5	11.1	NONE	-	34.6	34.9	34.7
M 1	0- 6	3	3	23.6	17.4 27.4	8 2	1633	DAY	13	3.3	3.4	3.3	3.4	3.3	NONE	-	31.6	31.6	31.6
M 2	0- 6	2	2	18.9	17.7 20.0	8 2	1726	DUSK	20	3.7	3.8	3.8	3.7	3.9	NONE	-	31.7	31.7	31.7
M 3	0- 6	2	2	16.6	15.8 17.4	8 2	1822	NIGHT	20	3.9	3.9	3.9	3.9	4.0	NONE	-	32.3	32.3	32.3
M 5	0-15	2	2	17.2	14.5 19.9	8 2	2018	NIGHT	139	12.2	17.0	16.0	17.0	10.0	STRONG	9-16	34.0	35.1	34.7
N 1	0- 6	6	6	20.3	17.5 23.0	9 2	0034	NIGHT	19	5.5	5.8	5.6	5.5	6.4	NONE	-	31.3	31.5	31.4
N 2	0-15	5	5	13.9	11.5 18.0	9 2	0126	NIGHT	24	7.9	8.6	8.1	7.9	8.6	NONE	-	32.7	33.1	33.0
N 3	0-15	49	49	13.7	7.1 29.8	9 2	0218	NIGHT	30	7.7	9.0	8.3	7.7	10.6	NONE	-	32.6	32.9	32.8
N 5	0-15	15	15	11.9	5.7 17.5	9 2	0509	NIGHT	82	19.2	19.4	19.3	19.4	16.6	NONE	-	35.3	35.5	35.5
N 5	18-33	6	6	11.5	8.6 13.4	9 2	0509	NIGHT	82	18.5	18.8	18.6	19.4	16.6	NONE	-	35.3	35.4	35.4
P 1	0- 6	3	3	14.9	13.6 17.3	9 2	1337	DAY	16	6.5	6.5	6.5	6.5	7.1	NONE	-	33.5	33.5	33.5
P 2	0- 6	9	9	21.1	14.6 26.6	9 2	1244	DAY	17	7.2	7.6	7.4	7.6	6.5	NONE	-	33.2	33.3	33.3
P 3	0- 6	108	108	14.8	6.5 23.9	9 2	1154	DAY	17	9.1	9.6	9.3	9.6	9.1	NONE	-	33.8	33.9	33.8
P 4	0-15	45	44	12.6	7.1 17.9	9 2	1033	DAY	31	14.1	17.0	15.8	17.0	13.1	WEAK	7-10	34.9	35.4	35.2
P 5	0-15	21	21	10.1	7.0 16.0	9 2	0848	DAY	60	20.0	20.0	20.0	20.0	17.8	NONE	-	35.5	35.6	35.5
P 5	18-33	5	5	10.5	6.5 15.4	9 2	0848	DAY	60	19.6	19.9	19.8	20.0	17.8	NONE	-	35.4	35.5	35.5
D66 3	(M)			(MM TL)		1966 D M	(EST)		(M)							(M)			
J 3	0- 6	1	1	29.4		16 4	0825	DAY	19	8.9	8.9	8.9	8.9	8.5	NONE	-	31.8	31.8	31.8
K 1	0- 6	2	2	27.3	25.3 29.3	19 4	1528	DAY	17	10.3	10.4	10.4	10.3	10.4	NONE	-	31.0	31.4	31.2
L 1	0- 6	1	1	25.0		20 4	0635	DAY	17	9.6	10.7	10.1	10.7	9.2	NONE	-	30.3	30.7	30.4
M 1	0- 6	12	12	22.7	20.6 24.7	20 4	1001	DAY	16	11.3	11.6	11.5	11.6	11.0	NONE	-	30.1	30.6	30.3
N 1	0-15	3	3	15.2	14.1 17.0	20 4	1753	DAY	21	10.7	12.2	10.9	12.2	10.7	WEAK	0- 4	32.2	32.6	32.4
N 2	0- 6	1	1	14.0		20 4	1851	NIGHT	22	11.7	11.8	11.8	11.8	11.9	NONE	-	32.1	32.1	32.1
N 3	0-15	9	9	15.0	11.0 17.4	20 4	1948	NIGHT	29	9.9	12.5	11.3	12.2	9.9	STRONG	6-10	31.7	32.2	32.0
N 3	18-24	4	4	15.3	14.4 16.0	20 4	1948	NIGHT	29	9.9	10.0	10.0	12.2	9.9	STRONG	6-10	32.1	33.9	32.7
N 4	0-15	1	1	19.0		20 4	2125	NIGHT	49	20.9	21.0	21.0	21.0	18.5	NONE	-	35.5	35.6	35.6

APPENDIX TABLE—Continued.

CRUISE STAT.	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE	MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (O/OO) RANGE	MEAN
D66 5	(M)			(MM TL)			1966 D M	(EST)		(M)						(M)		
J 2	0- 6	1	1	25.0			21 5	0505	DAY	14	13.7 15.2	14.3	15.2	13.5	WEAK	3- 4	28.4 31.2	30.0
J 3	0- 6	1	1	25.0			21 5	0547	DAY	19	13.9 16.9	15.3	16.9	13.0	STRONG	1- 5	25.9 30.7	28.6
K 1	0- 6	1	1	26.0			21 5	2119	NIGHT	18	12.8 16.3	14.4	16.3	11.8	STRONG	1- 6	29.7 30.4	30.1
D66 7	(M)			(MM TL)			1966 D M	(EST)		(M)						(M)		
E 1	0- 3	1	1	13.7			29 6	0705	DAY	14	15.8 17.1	16.4	17.1	14.7	NONE	-	32.0 32.1	32.0
F 1	0- 6	11	11	9.5	7.8	14.4	28 6	0833	DAY	17	18.5 18.5	18.5	18.5	18.5	NONE	-	30.8 30.9	30.8
F 2	0- 6	2	2	8.0	8.0	8.1	28 6	0917	DAY	24	18.5 18.7	18.6	18.7	14.9	NONE	-	30.3 30.6	30.5
D6610	(M)			(MM TL)			1966 D M	(EST)		(M)						(M)		
B 1	0-15	1	1	5.6			6 8	1249	DAY	20	17.5 18.5	17.7	18.5	17.5	NONE	-	30.1 30.3	30.2
C 1	0- 6	3	3	8.6	8.1	9.1	6 8	2343	NIGHT	19	19.8 20.6	20.5	20.6	12.3	STRONG	5-13	30.6 30.8	30.7
C 2	0-15	1	1	7.7			7 8	0037	NIGHT	28	13.3 20.2	18.2	20.2	9.6	WEAK	5-19	30.6 30.8	30.7
C 3	0-15	2	2	9.8	9.3	10.3	7 8	0139	NIGHT	32	14.5 20.3	18.8	20.3	7.9	STRONG	11-22	30.6 30.7	30.7
D 5	0-15	1	1	10.6			8 8	1515	DAY	37	20.1 22.2	21.5	22.2	8.6	STRONG	14-19	30.9 31.0	30.9
D6612	(M)			(MM TL)			1966 D M	(EST)		(M)						(M)		
A 2	0-15	1	1	8.0			1510	0209	NIGHT	30	14.0 14.3	14.2	14.3	12.9	NONE	-	31.2 31.3	31.2
A 2	18-24	4	4	4.4	4.1	4.7	1510	0209	NIGHT	30	13.2 13.9	13.6	14.3	12.9	NONE	-	31.3 31.5	31.4
A 4	0-15	1	1	9.3			1510	0615	DAY	49	14.2 14.3	14.2	14.3	10.1	STRONG	30-35	31.0 31.3	31.2
B 2	0-15	15	15	13.7	6.9	18.7	1410	1937	NIGHT	35	13.5 15.1	14.2	15.1	12.7	NONE	-	30.9 31.3	31.1
B 2	18-24	9	7	5.3	3.6	8.2	1410	1937	NIGHT	35	12.7 13.4	13.2	15.1	12.7	NONE	-	31.3 31.3	31.3
B 3	0-15	24	22	11.7	4.4	18.7	1410	2034	NIGHT	45	15.7 16.1	16.0	15.7	9.8	WEAK	25-39	31.3 31.5	31.4
B 3	18-33	31	27	5.9	4.0	11.1	1410	2034	NIGHT	45	12.9 15.9	14.8	15.7	9.8	WEAK	25-39	31.4 31.6	31.5
B 4	0-15	8	8	9.7	7.1	11.3	1410	1306	DAY	60	15.4 15.6	15.4	15.6	8.0	STRONG	29-42	30.7 31.0	30.9
B 4	18-33	2	2	9.8	9.7	10.0	1410	1306	DAY	60	13.8 15.5	15.3	15.6	8.0	STRONG	29-42	30.9 31.6	31.3
B 5	0-15	9	9	13.1	9.3	16.2	1410	1138	DAY	71	14.9 15.2	15.0	15.2	7.4	STRONG	26-42	30.7 31.0	30.8
B 5	18-33	4	3	8.8	6.9	9.7	1410	1138	DAY	71	12.9 14.9	14.5	15.2	7.4	STRONG	26-42	31.0 31.5	31.2
B 6	0-15	1	1	9.6			1410	0750	DAY	81	15.1 15.2	15.1	15.2	9.1	STRONG	33-46	31.5 31.7	31.6
C 2	0-15	155	65	11.6	5.0	18.2	1310	0912	DAY	25	15.7 15.9	15.8	15.9	11.9	STRONG	19-23	30.9 31.0	31.0
C 3	0-15	398	153	11.5	7.7	16.2	1310	1007	DAY	31	16.2 16.4	16.3	16.3	10.5	STRONG	24-30	31.0 31.2	31.1
C 3	18-24	4	4	10.8	9.3	12.2	1310	1007	DAY	31	16.1 16.2	16.2	16.3	10.5	STRONG	24-30	31.0 31.3	31.2
C 4	0-15	19	18	11.3	5.4	17.4	1310	1133	DAY	38	15.7 16.0	15.8	16.0	9.1	STRONG	25-32	30.9 31.0	30.9
C 4	18-33	1	0				1310	1133	DAY	38	9.7 15.6	13.6	16.0	9.1	STRONG	25-32	31.0 31.6	31.4

APPENDIX TABLE—Continued.

CRUISE STAT.	TOW DEPTH (M)	LARVAE NUMBER TOTAL	LARVAE NUMBER MEAS.	LARVAE LENGTHS MEAN (MM TL)	LARVAE LENGTHS RANGE		DATE 1965 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	TEMPERATURE (°C) RANGE	TEMPERATURE (°C) MEAN	TEMPERATURE (°C) SURF.	TEMPERATURE (°C) BOT.	THERMOCLINE DEGREE	THERMOCLINE DEPTH (M)	SALINITY (0/00) RANGE	SALINITY (0/00) MEAN
D6612(CON'D)																		
D 1	0- 6	2	2	7.6	5.1	10.2	610	0124	NIGHT	18	17.2 17.3	17.3	17.2	17.5	NONE	-	30.4 30.5	30.5
D 2	0- 6	5	5	6.9	4.4	8.7	610	0213	NIGHT	23	17.0 17.1	17.0	17.1	17.0	NONE	-	30.5 30.7	30.6
D 3	0-15	89	33	6.9	4.1	10.1	510	0308	NIGHT	24	16.8 17.0	16.9	17.0	16.8	NONE	-	30.8 30.9	30.8
D 4	0-15	24	17	8.1	4.7	12.8	1210	2336	NIGHT	27	16.3 16.4	16.4	16.4	15.4	NONE	-	30.8 31.2	31.0
D 4	18-24	105	41	6.8	4.7	12.8	1210	2336	NIGHT	27	15.4 16.2	15.9	16.4	15.4	NONE	-	31.0 31.3	31.2
D 5	0-15	11	10	7.8	5.0	10.0	1210	2204	NIGHT	36	16.5 16.6	16.6	16.6	11.0	WEAK	23-37	31.2 31.3	31.2
D 5	18-24	50	50	6.5	3.1	12.5	1210	2204	NIGHT	36	15.5 16.4	16.1	16.6	11.0	WEAK	23-37	31.2 31.4	31.3
D 6	0-15	17	17	12.0	9.3	13.7	1210	1801	NIGHT	54	16.4 16.4	16.4	16.4	7.4	STRONG	19-24	31.5 31.8	31.7
D 6	18-33	11	11	11.4	9.5	13.0	1210	1801	NIGHT	54	8.3 15.5	10.8	16.4	7.4	STRONG	19-24	31.1 31.7	31.3
E 1	0- 6	10	9	7.2	5.6	8.7	510	1501	DAY	16	17.7 17.9	17.8	17.7	17.9	NONE	-	30.3 30.6	30.4
E 3	0- 6	6	6	5.9	4.0	10.3	510	1323	DAY	22	17.4 17.4	17.4	17.4	16.9	NONE	-	30.8 30.9	30.8
E 4	0-15	3	2	11.5	10.0	13.0	1110	2034	NIGHT	29	16.4 17.2	17.0	17.2	13.0	STRONG	21-28	30.8 31.3	31.0
E 5	0-15	476	111	7.2	3.7	12.5	1110	2210	NIGHT	35	16.4 16.6	16.5	16.6	9.0	STRONG	22-31	31.2 31.4	31.3
E 5	18-24	563	99	6.6	2.9	13.7	1110	2210	NIGHT	35	15.3 16.4	16.0	16.6	9.0	STRONG	22-31	31.4 31.4	31.4
E 6	0-15	66	36	10.4	7.7	13.0	1210	0150	NIGHT	43	15.8 16.2	16.1	16.2	7.9	STRONG	19-24	31.2 31.5	31.4
E 6	18-33	9	9	9.6	4.9	12.2	1210	0150	NIGHT	43	7.9 15.4	10.4	16.2	7.9	STRONG	19-24	30.9 31.9	31.4
E 7	18-33	4	4	10.3	10.0	10.5	1210	0352	NIGHT	65	11.0 17.1	15.7	17.2	6.2	STRONG	26-39	31.7 32.3	32.1
F 4	0-15	4	4	6.2	4.7	6.9	510	0227	NIGHT	22	17.7 18.0	17.8	18.0	17.7	NONE	-	30.8 30.9	30.8
F 5	0-15	18	16	6.9	5.0	11.4	410	2151	NIGHT	35	17.4 17.9	17.7	17.9	14.2	WEAK	18-24	30.7 30.9	30.8
F 5	18-24	30	29	7.1	5.0	12.5	410	2151	NIGHT	35	14.9 17.0	16.1	17.9	14.2	WEAK	18-24	30.9 30.9	30.9
F 6	0-15	92	43	7.0	5.8	10.2	410	1953	NIGHT	54	16.4 17.3	17.0	17.3	6.8	STRONG	15-23	30.9 31.2	31.1
F 6	18-33	9	6	7.2	6.9	7.6	410	1953	NIGHT	54	7.5 14.4	9.9	17.3	6.8	STRONG	15-23	30.8 31.3	31.0
F 7	0-15	426	38	6.6	3.1	8.5	410	1552	DAY	91	17.8 18.2	18.1	18.2	10.2	WEAK	14-42	31.6 31.9	31.8
F 7	18-33	2	2	6.7	5.8	7.6	410	1552	DAY	91	10.6 16.8	14.3	18.2	10.2	WEAK	14-42	31.4 31.7	31.5
G 3	0-15	1	1	11.6			310	2231	NIGHT	22	18.2 18.3	18.3	18.2	18.3	NONE	-	31.0 31.0	31.0
G 4	0-15	2553	116	6.4	2.7	10.5	410	0627	DAY	31	18.1 18.2	18.2	18.2	15.8	NONE	-	31.0 31.1	31.0
G 5	0-15	79	37	7.1	2.7	10.3	410	0816	DAY	51	17.4 18.0	17.8	18.0	9.4	STRONG	19-26	30.9 31.0	30.9
G 5	18-33	2	2	7.3	7.2	7.4	410	0816	DAY	51	10.9 16.9	12.9	18.0	9.4	STRONG	19-26	31.0 31.2	31.1
G 6	0-15	29	24	7.0	3.9	9.7	410	1209	DAY	85	19.1 19.4	19.2	19.1	11.7	STRONG	26-40	31.5 31.9	31.7
G 6	18-33	6	5	7.4	6.3	10.3	410	1209	DAY	85	15.9 19.5	18.7	19.1	11.7	STRONG	26-40	31.8 32.3	32.1
H 4	0-15	10	10	10.3	8.0	11.3	310	1114	DAY	28	19.3 19.4	19.3	19.3	19.4	NONE	-	30.0 30.9	30.7
H 5	0-15	1	1	7.8			310	0950	DAY	39	19.6 19.7	19.7	19.7	14.0	NONE	-	30.8 30.9	30.9
H 5	18-33	5	5	7.4	6.9	8.0	310	0950	DAY	39	16.1 18.6	17.2	19.7	14.0	NONE	-	30.9 31.1	31.0
J 2	0- 3	2	2	5.9	5.5	6.4	110	1351	DAY	11	21.6 21.6	21.6	21.6	21.2	NONE	-	27.8 29.1	28.5
J 3	0- 6	2	2	3.9	3.5	4.4	110	1257	DAY	17	21.9 22.0	21.9	22.0	21.8	NONE	-	28.4 28.8	28.5
K 2	0-15	2	2	3.6	3.5	3.7	110	0825	DAY	22	21.4 22.0	21.9	22.0	18.9	WEAK	15-21	30.0 30.7	30.2
K 3	0-15	11	10	6.4	4.5	7.7	110	0924	DAY	25	19.9 21.9	21.5	21.9	16.3	WEAK	12-22	29.9 30.9	30.3

APPENDIX TABLE—Continued.

CRUISE STAT. D6614	TOW DEPTH (M)	********* LARVAE ********* NUMBER TOTAL	MEAS.	LENGTHS MEAN (MM TL)	RANGE		DATE 1966 D M	TOW START TIME (EST)	LIGHT COND.	WATER DEPTH (M)	*** TEMPERATURE (°C) *** RANGE		MEAN	SURF.	BOT.	THERMOCLINE DEGREE	DEPTH (M)	SALINITY (0/00) RANGE		MEAN
C 2	0- 6	1	1	22.0			312	0645	DAWN	28	9.8	9.9	9.9	9.8	9.9	NONE	-	32.9	33.0	33.0
C 3	0-15	1	1	21.5			312	0537	NIGHT	34	10.1	10.3	10.1	10.3	10.1	NONE	-	33.0	33.1	33.1
D 1	0- 6	2	2	21.7	20.0	23.5	112	1854	NIGHT	14	9.4	9.4	9.4	9.4	9.3	NONE	-	32.1	32.3	32.2
E 1	0- 6	5	5	19.9	18.5	20.5	911	2248	NIGHT	11	12.5	12.6	12.6	12.5	12.8	NONE	-	31.1	31.3	31.2
F 1	0- 6	1	1	21.0			1111	0602	NIGHT	18	13.5	13.5	13.5	13.5	13.5	NONE	-	31.4	31.8	31.6
F 2	0- 6	3	3	20.7	19.5	21.5	1111	0515	NIGHT	20	13.6	14.3	14.0	13.6	13.9	NONE	-	31.8	31.9	31.8
F 3	0-15	2	2	15.2	15.0	15.5	1111	0432	NIGHT	26	14.5	14.7	14.6	14.7	14.2	NONE	-	32.5	32.8	32.6
G 1	0- 6	100	55	20.7	17.0	25.0	1111	1604	DAY	10	14.5	15.0	14.7	15.0	14.3	NONE	-	32.4	32.4	32.4
G 2	0- 6	5	5	16.5	14.5	18.0	1111	1657	NIGHT	17	14.4	15.0	14.6	15.0	14.0	NONE	-	32.6	32.6	32.6
G 3	0-15	5	5	18.6	15.0	24.0	1111	1753	NIGHT	16	15.2	15.7	15.5	15.6	15.5	NONE	-	32.6	32.9	32.8
G 4	0-15	1	1	5.0			1111	1919	NIGHT	29	15.0	15.5	15.4	15.4	13.0	NONE	-	32.9	33.1	33.1
G 5	0-15	1	1	9.3			1111	2234	NIGHT	49	14.3	14.8	14.6	14.8	10.5	STRONG	26-28	33.3	33.5	33.4
H 1	0- 6	1	1	15.0			1211	1312	DAY	10	14.7	14.9	14.8	14.9	14.7	NONE	-	32.0	32.2	32.1
H 3	0- 6	1	1	5.7			1211	1041	DAY	25	15.8	15.9	15.9	15.8	15.3	NONE	-	32.6	32.8	32.7
H 4	0-15	2	2	13.7	13.5	14.0	1211	0918	DAY	29	14.9	15.6	15.2	15.6	14.7	NONE	-	32.8	33.4	33.1
H 5	18-33	2	2	5.3	5.0	5.7	1211	0754	DAY	42	14.0	14.3	14.2	15.3	14.0	NONE	-	33.8	33.9	33.9
H 7	0-15	1	1	19.0			1211	0503	NIGHT	134	14.5	15.1	14.7	14.5	11.2	STRONG	43-52	33.8	34.6	34.0
J 2	0- 6	1	1	20.5			1311	0036	NIGHT	10	15.1	15.3	15.2	15.1	15.2	NONE	-	31.7	32.0	31.8
J 3	0- 6	1	1	10.6			1311	0202	NIGHT	16	15.0	15.2	15.1	15.2	15.3	NONE	-	32.3	32.4	32.4
J 4	0-15	6	6	9.3	7.4	12.5	1411	1348	DAY	22	14.9	15.0	14.9	14.9	15.0	NONE	-	33.2	33.3	33.2
K 1	0- 6	17	17	15.1	4.4	22.0	1811	0842	DAY	15	14.5	14.5	14.5	14.5	14.6	NONE	-	33.2	33.3	33.2
K 2	0-15	1	1	12.5			1811	0929	DAY	20	14.1	14.7	14.4	14.2	14.7	NONE	-	32.3	33.8	33.2
K 3	0-15	1	1	6.0			1811	1022	DAY	24	14.7	14.7	14.7	14.7	14.9	NONE	-	33.6	34.0	33.8
K 4	18-24	2	2	11.5	10.6	12.5	1811	0325	NIGHT	33	14.4	14.6	14.5	14.7	14.5	NONE	-	34.1	34.1	34.1
K 5	0-15	1	1	13.1			1811	0155	NIGHT	37	14.5	14.8	14.7	14.8	13.9	NONE	-	34.2	34.4	34.3
L 1	0- 6	3	3	10.9	10.2	11.9	1711	0838	DAY	21	14.2	14.4	14.3	14.2	15.1	NONE	-	31.0	31.6	31.2
L 2	0- 6	2	2	13.7	10.5	17.0	1711	0754	DAY	21	15.0	15.2	15.1	15.2	15.0	NONE	-	33.3	33.5	33.4
L 3	18-24	1	1	11.9			1711	0707	DAY	32	14.8	15.0	14.9	15.1	15.0	NONE	-	33.3	33.8	33.5
M 1	0- 6	43	43	9.7	6.6	14.0	1611	1530	DAY	26	14.8	14.9	14.8	14.9	14.7	NONE	-	33.4	33.5	33.5
M 2	0- 6	67	37	8.0	5.0	11.4	1611	1440	DAY	20	14.9	15.1	15.0	15.1	15.0	NONE	-	33.7	33.8	33.7
M 4	0- 6	10	10	9.8	6.5	11.4	1611	2339	NIGHT	41	17.5	17.6	17.5	17.6	17.9	NONE	-	35.0	35.1	35.1
N 1	0- 6	1	1	10.7			1611	1034	DAY	25	16.4	16.4	16.4	16.4	16.4	NONE	-	34.0	34.0	34.0
N 2	0-15	14	14	9.0	4.3	11.4	1611	0937	DAY	26	18.6	18.8	18.7	18.8	18.9	NONE	-	35.5	35.6	35.6
N 3	0-15	3	3	7.2	5.1	11.1	1611	0833	DAY	30	19.3	19.5	19.4	19.3	19.4	NONE	-	35.6	35.8	35.8

AGE AND GROWTH OF PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

THOMAS A. DARK[1]

ABSTRACT

The age and growth of Pacific hake, *Merluccius productus*, collected off California, Oregon, and Washington in 1964-69, were studied.

The age determination procedure was examined and considered to provide valid ages.

Several sources of variation in the age structure of the population were given cursory examination. Relative size of the year class and sampling area (average age tends to increase with latitude) contribute substantially to the variation of the population age composition while sex and sampling season have lesser effects.

Growth in length is rapid during the first 3 yr after which it slows and approaches an asymptote in the oldest ages, 10-13 yr. Females have a faster rate of growth than males and tend to survive 2 or 3 yr longer, to age 13. Growth in length can be adequately described by the von Bertalanffy growth equations: $l_t = 56.29\ (1-e^{-0.39\ (t-0.20)})$ for males and $l_t = 61.23\ (1-e^{-0.30\ (t-0.01)})$ for females. Year class variation in growth rate was detected by back-calculation, using the body length (Y) -otolith radius (X) relationship $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$. Growth in weight was determined by use of the length-weight equations: $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females. Males attain an average weight of about 1,211 g by age 11 and females reach an average weight of 1,374 g by age 13. Annual instantaneous growth rates in weight were computed and were found to decrease most during the fourth year for both sexes and very little growth occurred after the sixth year for males or after the ninth year for females.

The Pacific hake, *Merluccius productus*, is a common gadid fish that ranges from the Gulf of California to the Gulf of Alaska (Hart 1973) but is most abundant from Baja California to southern British Columbia (Alverson et al. 1964). There is apparently a single population offshore and another in Puget Sound, Wash. (Utter and Hodgins 1971). The Puget Sound population supports only a small fishery and is not considered in this report.

Feeding adult hake are usually found over the continental shelf and exhibit pronounced diel movement. During the day they are most commonly found in compact schools near the seabed, but as darkness approaches the schools rise and become more loosely structured. During their spawning period mature hake are more pelagic in behavior than during the rest of the year. They apparently spawn at intermediate depths in water 1,000 m deep or more and demonstrate little diel movement (Nelson 1967). Spawning occurs from January through April off northern Mexico and southern California (Ahlstrom and Counts 1955). Eggs and larvae are pelagic and are found mostly near the thermocline at depths of about 45 to 100 m. It is not clear at what age juvenile hake leave their pelagic phase and become more closely associated with the seabed. One-year-old hake are found in inshore waters off southern California, associated at times with schools of northern anchovy, *Engraulis mordax* (Dark et al. 1970). Hake, 1 to 3 yr old, are taken in shrimp trawls along the Oregon and California coasts (Morgan and Gates 1961). Pacific hake less than 4 yr old are rarely found north of Oregon. Most 4- to 13-yr-old hake mature and are found feeding off the coasts of Oregon, Washington, and southern British Columbia during the spring and summer. By early winter only a small portion of the summer population remains in these areas.

Temporal and areal distribution of the various life history stages suggest that adult Pacific hake undertake extensive annual migrations along the west coast of North America (Alverson and Larkins 1969). Most adult hake seem to move northward along the coasts of California, Oregon, and Washington in early spring on a feeding migration as far north as central Vancouver Island. In late fall the adults begin a return

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migration to the south which terminates in the spawning area off southern California and Mexico. The eggs and larvae drift onto the continental shelf and the young inhabit the waters of California and Oregon as 1-to-3 yr-olds. Some 3-yr-olds and most 4-yr-olds become sexually mature (Best 1963) and are recruited to the adult population.

Pacific hake were landed in small quantities in California ports as early as 1879. California landings from 1916 to 1951 varied from about 0.2 to 90 metric tons. An animal food fishery developed in 1952 creating an increased demand for low value species and hake landings increased to about 590 metric tons in 1956. From 1956 to 1968, landings averaged about 200 metric tons annually.

Prior to 1965 Washington and Oregon fishermen did not purposefully fish for hake and, in fact, considered them a nuisance species. In 1965 a small fishery was initiated under the guidance of the U.S. Bureau of Commercial Fisheries (BCF)[2] to examine the feasibility of efficiently harvesting Pacific hake off Washington and Oregon. Four vessels began fishing commercially in 1966 because favorable results were obtained from the feasibility study and a new fish reduction plant had begun operations at Aberdeen, Wash. During the same year a large Soviet trawl fleet appeared off the Washington-Oregon coast fishing for rockfish, *Sebastes* spp., and Pacific hake. Competition from the Soviet fleet was so severe that it seriously threatened the existence of the U.S. fishery. Negotiations between the United States and the Soviet Union in February 1967 resulted in an agreement which restricted the size of the Soviet fishing area off the southern Washington coast. The U.S. fleet was more successful in 1967 because of a reduction of Soviet competition and increased efficiency of U.S. vessels. This greater efficiency stemmed from the increased experience of fishermen, improved fishing gear, and greater scouting capability. The total U.S. catch in 1967 was 8,381 metric tons (catch-per-unit-effort [CPUE] = 4.5 metric tons/h), as compared to a total catch of 1,694 metric tons (CPUE = 3.0 metric tons/h) in 1966 (Nelson 1970). Soviet catches in 1966 and 1967 were about 136,050 and 170,590 metric tons, respectively. Since 1967 the Soviets have continued to fish for Pacific hake and annual catches have averaged about 140,000 metric tons. The U.S. fishery was discontinued in 1968 when the reduction industry, facing a depressed fish meal market, was unable to give vessel owners prices that were competitive with those offered by the shrimp and groundfish processors (Pereyra and Richards 1970).

An agreement pertaining to the joint exploitation of groundfish in the northeast Pacific Ocean was negotiated between the United States and the Soviet Union in 1967 and renegotiated in 1969 and 1971. Scientific meetings have been held annually to discuss problems of mutual concern such as assessing the size of the Pacific hake population, determining the effects of the fishery, and estimating rates of growth, mortality, and maximum sustainable yield. Recommendations resulting from the scientific meetings provide a basis for modification of the bilateral fishery agreement—which can be done every 2 yr.

Initial growth estimates were based on preliminary data but served to provide essential real time estimates of maximum sustainable yield. Subsequently, additional data have been collected allowing for refinement of early growth estimates. The objectives of the present study were to provide new estimates of the growth rate of Pacific hake and to examine some of the potential sources of variation. An analysis was made of the reliability of the age determination method used since age information is basic to growth studies. The variability in the age structure of the Pacific hake population was also examined since age composition is frequently used to evaluate relative year class strengths, mortality rates, and the effects of fishing.

SAMPLING

Collection Methods

Biological data were collected from two sources: "commercial" samples from the commercial fishery and "research" samples taken aboard research vessels.

Commercial samples were taken mainly in 1966-67 when a U.S. hake fishery was conducted off the Washington coast during May-September. A sampling station was established at the reduction plant in Aberdeen, Wash., where essentially all hake taken off Washington and Oregon were landed. An attempt was made to man the station every other week and to sample the catches as they were unloaded at the plant. Irregular landing schedules, especially in 1966, resulted in sporadic

[2]Presently, the National Marine Fisheries Service.

sampling. In some sampling weeks, landings were made during 3 or 4 days while in other weeks there were no landings. Landings were sampled as fish moved from the vessel to the plant over a conveyor system. Approximately 200 specimens were collected for each sample. Specimens were first dissected to determine the sex, then were measured (to the nearest centimeter) from the snout to the fork of the tail. An otolith was removed for age determination and, when time allowed, whole specimens were weighed to the nearest decagram.

To simplify the collection of otoliths, most otolith samples were stratified by 1-cm body length intervals. Otoliths were taken from five males and five females in each length interval until the sample was exhausted. Although average length-at-age information can be taken directly from such stratified samples, randomization was necessary to obtain unbiased estimates of age composition.

Research vessel samples were collected from 1964 through 1969 and were both stratified and random. Most research vessel samples were processed at sea for the same biological data as those taken from commercial samples. When weights were taken a small hand-held steelyard was used which provided more consistent readings than did spring scales.

The research vessel samples used herein are geographically and temporally restricted simply because it was beyond the capability of a single vessel to conduct more extensive sampling. The samples taken at the reduction plant in 1966-67 provided the best temporal coverage over a season, but their areal distribution was restricted mainly to fishing grounds off Grays and Willapa Harbors, Wash.

Sample Representativeness

Whereas the nature of available samples places constraints on some aspects of the following study, the large number and size of samples collected over several years and over a large part of the species' geographical range render them valuable in examining the reliability of earlier estimates of growth (Best 1963; Tillman 1968). Also, some of the more conspicuous variations in both growth rates and age composition can be examined.

Figure 1 gives a general representation of the distribution of sampling effort in 1964-69. The adult portion of the population (4- to 13-yr-olds) occurring off the coast of Washington during the summer was the most intensively sampled, especially in 1966-67 when commercial samples were taken. Research vessels sampled adults off Washington, Oregon, and California, mostly during the summers of 1965-67. Juveniles (1- to 3-yr-olds) were sampled only sporadically and much less intensively. In the winters of 1965 and 1968, research vessels searching off southern California and northern Mexico for spawning hake obtained some samples of 1- and 2-yr-old specimens. Very few 3-yr-old hake were captured, probably because there was relatively little sampling effort in areas where they were likely to be most abundant.

Commercial vessels fishing for Pacific hake off Washington used Cobb pelagic and BCF universal trawls (Johnson and High 1970). The stretched mesh size varied from 5.1 to 7.6 cm in the trawl bodies and cod ends. Research vessels used the

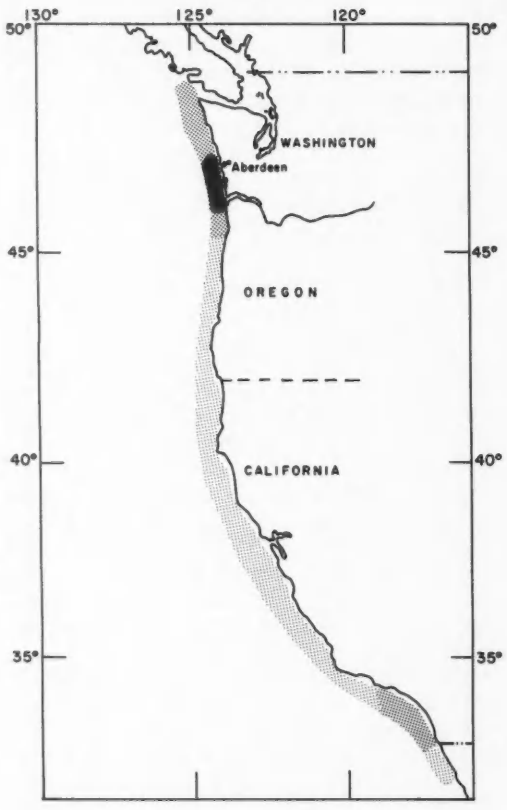


FIGURE 1.—Distribution of sampling effort for Pacific hake, 1964-69. (Darker stipling infers more intensive sampling.)

same trawls, but with 3.8-cm liners in the cod ends much of the time. Liners were used to determine the availability of the youngest age groups. Research and commercial samples were never taken in such a manner that length frequencies could be compared to isolate the effects, if any, of the 3.8-cm liner. But there was probably no significant selection for fish length without the liner since similar unlined trawls used in the Puget Sound hake fishery apparently retain all fish of 35 cm or greater.[3] Because very few hake off Washington were as small as 35 cm, sampling gear differences were not considered to be a significant source of sampling error. Therefore research and commercial samples taken in 1966-67 were combined at times to increase sample sizes and to improve temporal and areal sampling coverage.

DETERMINATION OF AGE COMPOSITION

Aging Technique

A prerequisite to any growth study is a method for reliably determining the age of individual fish. European investigators (Birtwistle and Lewis 1925; Hickling 1933; Bagenal 1954) found the otolith to be the most useful structure in determining the age of the European hake, *Merluccius merluccius*. Bigelow and Schroeder (1953) arrived at the same conclusion while studying the silver hake, *M. bilinearis*. Apparently Best (1963) was the first to age Pacific hake. He found that from the standpoint of availability otoliths were superior to scales as most scales were absent on trawl-caught specimens.

Our collection of otoliths was standardized in an effort to control sampling variation. Samplers attempted to always collect the otolith from the right side of the head to avoid any confounding effects due to possible otolith asymmetry. If the right otolith was damaged during the extraction process, the left otolith was accepted as an alternate (5-10% of all samples). Otoliths were thoroughly cleaned and preserved in a solution of 10-30% ethyl alcohol. Occasionally otoliths with a uniform chalky appearance were encountered and were cleared by dipping them in a weak solution of hydrochloric acid. This practice was followed with care to prevent the dissolution of annuli at the otolith edge.

Otoliths were placed in a petri dish with the bottom painted black, illuminated with a reflected light, and read under a dissecting microscope at a magnification of 6.6×. Each otolith was read by two readers and if the ages did not agree, as was the case in 25-40% of the otoliths processed, the otolith was examined by a third reader. The best estimate of age was taken as the age agreed upon by any two readers. When all three readers disagreed (about 5% of the readings), the middle reading was used. If one reader could not make a determination and agreement could not be reached by the other two, the otolith was considered unreadable. Generally there was a 3-5% rejection rate.

The majority of the hake otoliths were collected during the summer (May-September). Assuming that the past winter was represented by the last (most recent) translucent zone, the age was taken to be simply the total number of translucent zones on the otolith. The few winter (February-March) samples collected were composed mainly of fish completing their first or second year of life. The same aging criteria cited above were applied to winter samples, except those otoliths without a translucent zone were assigned to age "1" instead of "0." This was done on the premise that the translucent zone would have been deposited shortly after the sample was taken, since young of the year would not have been captured by the sampling gear.

Validity of Aging Technique

Because the use of otoliths in aging Pacific hake had not been completely evaluated, some attention was devoted to determining the reliability of the procedure. Graham (1929) gives three indirect methods of evaluating the use of scales and otoliths for age determination: 1) agreement with Petersen's (1895) method; 2) seasonal changes in scale or otolith margins; and 3) observation of a strong year class over a period of years.

The Petersen's (1895) method, which compares the relative abundance of age groups as determined by length distribution with age groups as determined by analysis of scales, otoliths, or other structures, is generally only applicable to the first three or four age groups. For Pacific hake, the length distributions of the age groups overlap extensively after age 3, restricting the use of the

[3]Larkins, H. A., H. H. Shippen, and K. D. Waldron. Features of a northern Puget Sound hake population. Unpubl. manuscr. Northwest Fish Cent., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash.

method to the first three age groups. Because few 2- and 3-yr-old hake were present in the samples, Petersen's (1895) method could not be effectively applied.

According to Graham's (1929) second method, observations of the development of translucent and opaque zones on the perimeter of the otolith (based on data from a population that had been sampled periodically during a year) may provide an indication of the frequency with which the zones are formed. A single occurrence of a particular zone during a year would provide an annual mark which may be suitable for age determination. In European hake (Hickling 1933) opaque zones have been associated with good physical condition and growth whereas translucent zones have been associated with a lesser physical well-being and retardation or cessation of growth. Poor condition can result from a decrease in the food supply, the onset of maturation and spawning, or both.

For the present study a special effort was made to record the zone type on the edge of all hake otoliths collected during 1967. Samples were taken during March, April, May, June, and August. Otoliths from a sample collected in November 1969 were added to the above spring and summer samples for data on the winter appearance of the edge. It appears that there are long and overlapping periods when zones are deposited because most samples had some otoliths with opaque margins and others with translucent margins. One exception is the small, March 1967 sample that contains only 1-yr-olds. Even though opaque edges are plainly recognizable in the young age groups, all otoliths in this sample had translucent margins.

The persistent occurrence during the summer (the apparent growing season) of otoliths with a translucent edge may be at least partly because the newly deposited opaque material is not always detectable due to the thinness of the edge and the resulting transparency.

Figure 2 demonstrates that the frequency of opaque edges decreases rapidly with the age of the fish. This is almost certainly a bias resulting from the increased difficulty in distinguishing the zone type on the edge of the otolith as the fish becomes older. Opaque bands on the otoliths of young fish (1-4 yr) growing at a relatively fast rate are wide, dense, and readily distinguishable. As growth slows in older specimens, new opaque zones become narrower, and are not always apparent

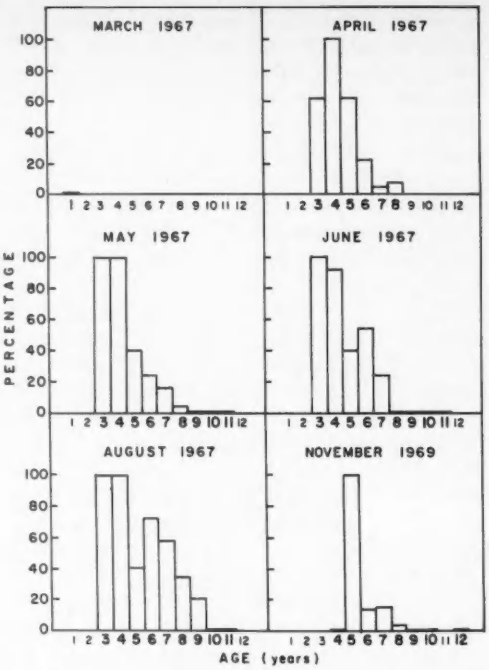


FIGURE 2.—Percentage of otoliths with opaque edges by age group (ages actually observed in bold print).

until late in the growing season or until bordered by a new translucent zone.

Because the zone type on the edge of the otolith is related to the age of the fish, a comparison of otoliths could be misleading if the sample age compositions vary to a large extent. Whereas the age compositions of the 1967 samples were similar, the age composition of the 1969 sample was noticeably different (Figure 3). To avoid the effects of advanced fish age on a reader's ability to accurately judge opaque zones at the otolith edge type, samples of 6-yr-olds taken in April-November and one sample of 1-yr-olds taken in March were compared in Figure 4. The graph suggests that Pacific hake start to deposit opaque material around April. The time of deposition may vary with age, but other age groups were not present in numbers adequate for comparison. The incidence of otoliths with opaque edges increased steadily through August when it peaked at about 72%. A dramatic decrease in otoliths with opaque edges occurred in the November sample. The foregoing analysis indicates that the physical well-being of Pacific hake improves in early spring

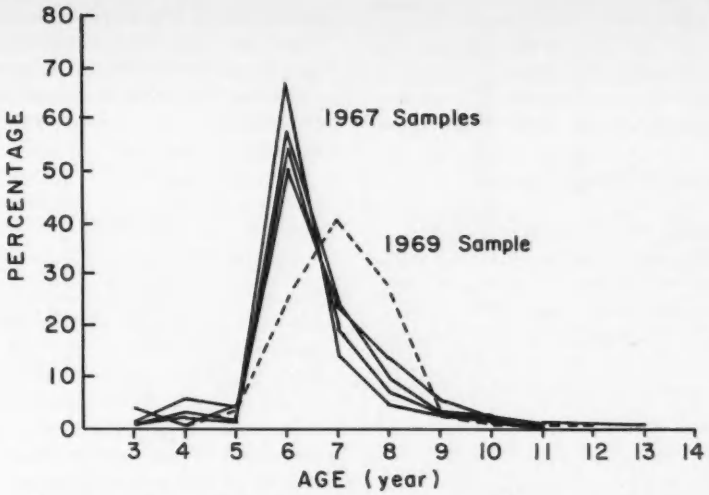


FIGURE 3.—Age composition of samples selected for analysis of zone type on the otolith edge.

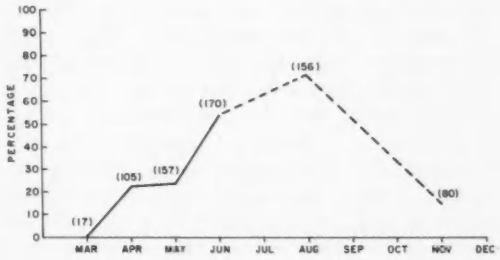


FIGURE 4.—Percentage of otoliths with opaque edges by month of collection, 1967-69. (Sample size occurs in parentheses.)

(indicated by the appearance of the opaque zone in the otolith edge). Growth occurs throughout the summer until sometime after August. The onset of maturation and the spawning migration in late fall probably place additional demands on the energies of the animal, resulting in slowed growth which is reflected in the appearance of the translucent zone at the otolith edge.

Although observations are not available during all months, the unimodal characteristic of the curve in Figure 4 strongly suggests that one opaque and one translucent zone are deposited each year and that the zones provide reliable annual marks. However, comprehensive monthly sampling is required to confirm unimodality.

The third method suggested by Graham (1929) is based on the rationale that if a predominant year class enters a population of fish and if the aging technique is reasonably reliable, then the year class should be observed progressing normally through the population age structure for several years.

Fortunately the 1961 year class of Pacific hake was extremely strong when it was partially recruited (designated as 4-yr-olds) to the adult hake population in 1965. In that year the 4-yr-olds comprised 15% of the adult population off Washington, while in other years from 1964 to 1969, 4-yr-olds contributed only 0-2%. In 1966 sampling indicated that over 50% of the adult population off Washington was composed of 5-yr-old hake. The dominance of the 1961 year class evidently continued through 1967, when over 70% of the population was 6-yr-olds; 1968 when about 64% was 7-yr-olds; and 1969 when about 24% was 8-yr-olds (Figure 5). In contrast, from 1964 to 1968, 8-yr-olds comprised only 2.4-13.7% of the population. This movement of the 1961 year class through the population age structure is accepted as additional evidence that the translucent zone represents a single annual mark.

Randomization of Age Samples

As noted previously some otolith samples used herein were collected aboard research vessels and are considered to be random, but the majority were commercial samples in which otoliths were

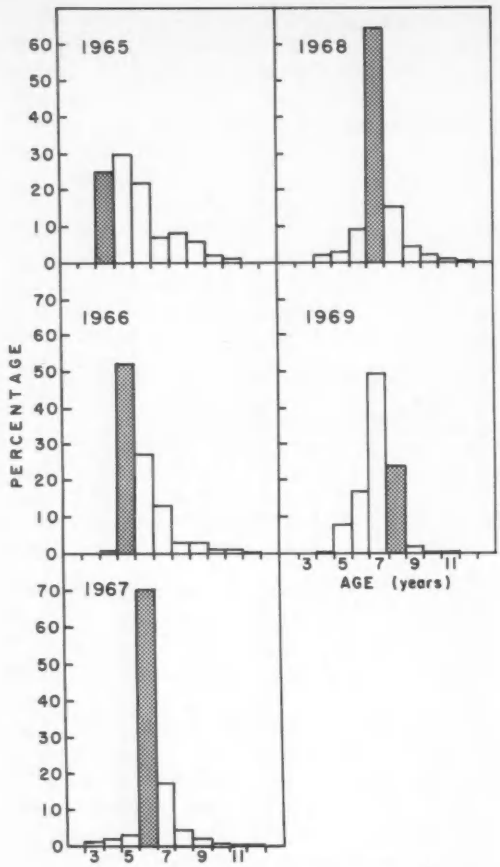


FIGURE 5.—Age composition of Pacific hake taken off Washington during May-August, 1965-69. (Shaded bar denotes the 1961 year class.)

collected in a stratified manner. Before the commercial samples could render representative age compositions, they had to be randomized. This was accomplished by constructing an age-length key for each sample. The percentage age frequency per length interval observed in stratified subsamples was applied to the length frequency distribution of the entire sample.

VARIABILITY IN AGE COMPOSITION

Several potential sources of variation in age composition were analyzed using research and commercial samples. Age composition is used for evaluation of the effects of fishing, estimation of recruitment, growth, and mortality. Therefore the major sources of sampling variation should be identified. The effects of annual, seasonal, latitudinal, and sexual variation are considered in this section.

Annual Variation

Annual variation in age composition was studied using samples collected off the Washington coast during May-September 1965-69. It has been assumed (Tillman 1968; Nelson and Larkins 1970) that Pacific hake are fully recruited to the fishery at age 5. If this assumption is valid and if recruitment and mortality rates are constant then one would expect, from a relatively unexploited population, a typical catch curve with the 5-yr-olds most numerous and the succeeding ages decreasing at a rate equal to the rate of natural mortality. This pattern was apparent in 1965 (Figure 5). The partially recruited 4-yr-olds were not as numerous as the 5-yr-olds which predominated. From age 5 there was a progressive decrease in the relative abundance of succeeding age groups until only a few 13-yr-olds remained. By examining the age compositions in subsequent years, it became obvious that the 4-yr-old age group in 1965 was considerably larger than usual. This was the first indication that the 1961 year class was unusually large. In 1966 the 1961 year class (5-yr-olds) was probably fully recruited and strongly dominated the age structure. The relative abundance of the incoming 1962 year class (4-yr-olds) was much smaller than the 1961 year class in the 1965 samples. The 1961 year class can be followed through the age composition in 1967-69. In 1969 the 1961 year class lost its dominance to the 1962 year class, but still produced extraordinarily large numbers of 8-yr-olds. Apparently the 1965-66 year classes were smaller than those observed previously since in the 1969 sample no 4-yr-olds were observed.

Obviously annual variation in age composition does occur in Pacific hake and is at least partly due to varying levels of recruitment of incoming year classes.

Seasonal Variation

In 1966-67 regular sampling of Pacific hake from off the southern coast (lat. 46°00′-46°59′N) of

Washington occurred throughout the fishing season. These samples were combined as "early" (collected in May-June), "middle" (July), and "late" (August-October) samples for the purpose of identifying any gross seasonal changes in age composition (Figure 6). The 1966 early sample contains somewhat fewer 5-yr-olds and more 6-yr-olds than either the middle or late samples which are very similar. For all practical purposes, the age compositions of the three 1967 samples are identical. There is little evidence in these comparisons to suggest that there is significant change in age composition during the time the Pacific hake are present in commercial quantities off southern Washington. The paucity of samples appropriate for further comparisons precludes assessment of seasonal age composition variation which may occur at other times and places.

Latitudinal Variation

Variation occurs in the age composition of Pacific hake samples taken from different portions of the latitudinal distribution (Nelson 1967; Tillman 1968). Table 1 is adapted from Tillman's table 14 to show the percentage age composition

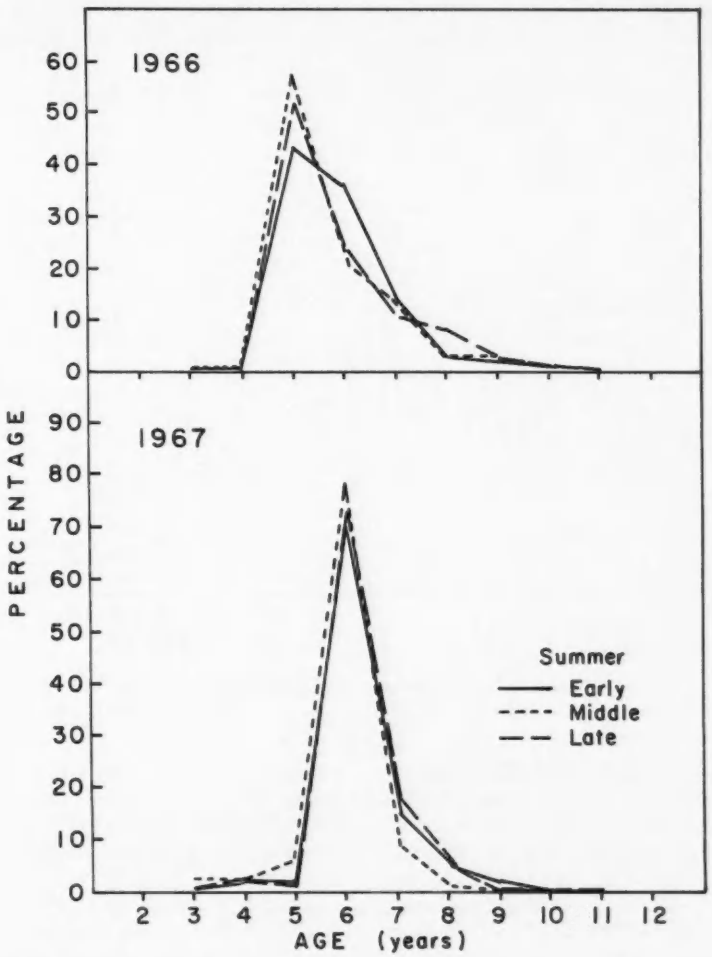


FIGURE 6.—Age composition of Pacific hake collected off southern Washington (lat. 46°00'-46°59'N) by early, middle, and late summer periods.

TABLE 1.—Age composition (percentage) of hake taken off Washington, Oregon, and California in 1965 by research vessels (adapted from Tillman 1968).

Age (years)	Washington			Oregon			California		
	Male	Female	Sexes combined	Male	Female	Sexes combined	Male	Female	Sexes combined
1	–	–	–	–	–	–	0.2	1.5	0.6
2	–	–	–	–	–	–	1.8	4.0	2.4
3	–	–	–	–	–	–	3.8	6.9	4.7
4	13.0	22.5	17.7	26.8	46.4	37.2	44.4	38.2	42.6
5	28.9	20.6	24.7	37.0	27.6	32.0	29.8	25.1	28.4
6	27.2	23.8	25.1	22.8	11.9	17.0	8.1	10.6	8.8
7	13.5	5.2	8.5	4.1	4.6	4.4	5.1	5.5	5.2
8	12.9	10.6	11.5	9.1	4.3	6.6	3.5	5.1	4.0
9	3.0	10.3	7.4	0.1	3.9	2.1	2.7	2.5	2.6
10	1.4	4.9	3.5	–	0.6	0.3	0.4	0.6	0.4
11	–	1.4	0.9	–	0.5	0.3	0.1	–	0.1
12	–	0.6	0.4	–	–	–	0.1	–	0.0
13	–	–	–	–	0.1	0.1	–	–	–
Sample size	1,474	2,196	3,670	810	914	1,724	1,586	670	2,256

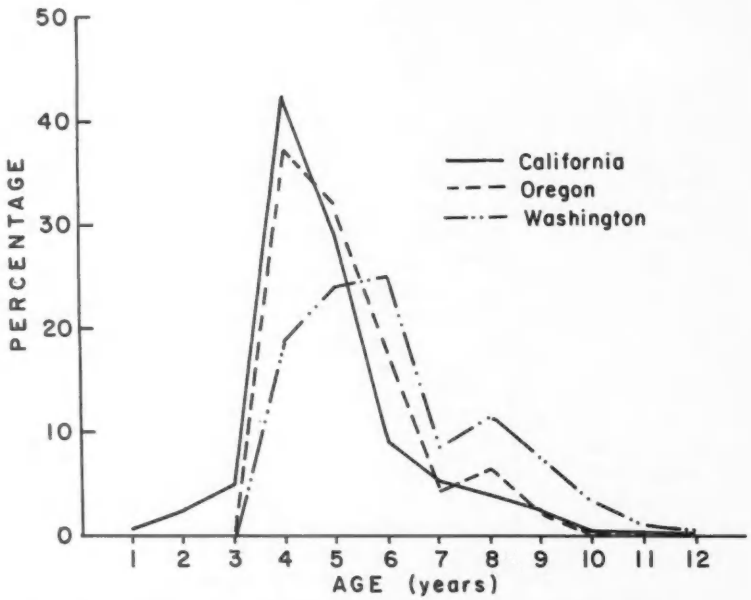


FIGURE 7.—Age composition of Pacific hake collected off California, Oregon, and Washington in 1965.

for research vessel samples taken off Washington, Oregon, and California in 1965. These samples were used because they provided the best geographic coverage and were taken with similar trawl gear, equipped with small-mesh cod end liners capable of capturing juvenile hake. The age composition of the California sample probably does not truly reflect the relative abundance of the age groups. The southern distribution and abundance of adult hake was a primary consideration at the time of sampling and, because the very young hake normally are not found associated with the adults, they probably were not taken in proportion to their abundance. Figure 7 shows, however, that samples taken off California included 1-, 2-, and 3-yr-olds, which did not occur in Washington and Oregon samples. Washington and Oregon samples composed of fish 4-yr-old and older were considered to be representative of the population in those areas. There is a smaller per-

centage of 4-yr-olds and a greater percentage of 5- and 6-yr-olds in the Oregon sample than in the California sample. Similarly, the Washington sample contains a much smaller percentage of 4-yr-olds and a greater percentage of nearly all the older age groups than does the Oregon sample. It cannot be clearly demonstrated whether there are in fact fewer 4-yr-olds in the hake population off Washington or whether additional older specimens are recruited, depressing the relative abundance of the 4-yr-olds. However, since 3-yr-old hake are not recruited to the Washington fishery and it is difficult to rationalize the sudden occurrence of additional large numbers of older, adult fish not found off Oregon and California, the most likely event is that the 4-yr-olds are only partially recruited off Washington and are not as numerous as they are off Oregon.

In May, July, and October 1965 and in August 1966, samples were available from off the Washington coast from lat. 46°00'N to 48°59'N. For each year the samples were grouped by half degree intervals of latitude and compared in Figure 8 to determine if changes in age composition among smaller spatial units than used in the foregoing discussion could be detected. The 1965 samples were collected during a period of several months but, as indicated in a previous section, seasonal (spring-fall) variation should not be a significant factor. Although there is considerable random variation in the relative abundance of an age group among areas, there appear to be some

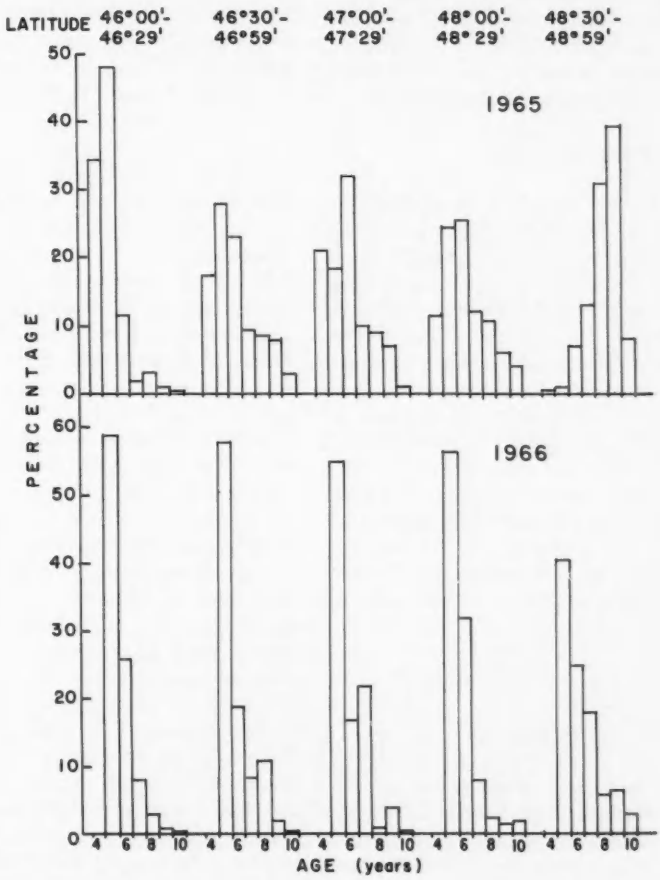


FIGURE 8.—Age composition of Pacific hake taken at various latitudes off Washington in 1965-66.

trends associated with latitude. Generally, the relative abundance of 4- and 5-yr-olds tended to decrease as sampling progressed from south to north while the relative abundance of 7- to 10-yr-olds tended to increase. This is consistent with observations over a larger sampling area.

In summary, 1-, 2-, and 3-yr-old Pacific hake are rarely encountered north of California and, as sampling progresses northward along the Washington coast, the younger age groups (4- and 5-yr-olds) contribute less to the population while the relative abundance of the older age groups (7- to 10-yr-olds) increases.

Such latitudinal stratification of age groups, apparently occurring to some extent even within 3 degrees of latitude, compounds the problem of representatively sampling the age composition of not only the entire hake population, but also the commercially available portion of the population. This spatial variation should be considered when comparing annual changes in age composition.

Sexual Variation

Pacific hake samples taken off Washington in 1965-69 were used to examine the variation in age composition between male and female components. The percentage of each sex by age group was calculated (Table 2) and plotted in Figure 9. The age compositions for males and females are similar in all years. The greatest difference occurred in 1965 when females contributed a larger proportion of the 4-yr-old group. In all years, a greater percentage of the females occurred in the older age groups (8 yr and older). These results correspond well with earlier observations (Best 1963; Tillman 1968) that females live longer and may be the sole survivors by age 11 and 12. Therefore sampling that is highly selective for sex would provide biased estimates of the relative abundance of older age groups.

GROWTH OF PACIFIC HAKE

Growth in Length

To determine the general shape of the growth curve for Pacific hake, average lengths-at-age by sex were computed using combined data from samples taken off Washington, Oregon, and California during 1965-69 (Table 3).

Growth of both sexes is quite rapid during the first 3 yr, then slows abruptly (Figure 10). Deceleration of the growth rate probably is not as pronounced as indicated. Latitudinal stratification of ages discussed previously is probably a result of stratification by size; therefore, mainly the larger members of the younger age groups would be recruited to the Washington-Oregon area where most samples were collected. Best (1963), for instance, computed the average lengths for small samples of hake (age groups 4-13 consisted of females only) taken off northern California and the 3- to 6-yr-olds were somewhat shorter than those in the Washington-Oregon samples (Figure 10). The most accurate growth curve for 2- to 6-yr-olds would probably fall somewhere between that based on Best's (1963) data and the curves generated from my data. Asymptotic growth has been shown for Cape hake, *M. capensis* (Botha 1969); silver hake (Fritz 1962); and Pacific hake in Puget Sound (see footnote 3). For the purpose of this study it is assumed that the growth curve for the length of coastal Pacific hake is also asymptotic.

Sexual differences in the size at age occur in most hake species (Hickling 1933; Hart 1948; Fritz 1962; Botha 1969), and the Pacific hake is no exception (Figure 10). Females are noticeably longer by age 4, but may be longer even at an earlier age. Larkins et al. (see footnote 3) reported that female Pacific hake of the Puget Sound population are slightly longer than males even as 1-yr-olds. This cannot be demonstrated for coastal hake because sex information was not available for 1-yr-olds and so few 2- to 3-yr-olds were collected that one cannot accept the estimated mean lengths by sex with confidence. Although sexual differences in growth exist, these differences are not large. The maximum difference in mean lengths is 3.12 cm occurring at 11 yr of age (Table 3).

Year class variation with respect to growth was examined by two means: 1) the comparison of age-length data collected in 1965-69, and 2) the back-calculation and comparison of growth rates for five year classes.

Mean body lengths by age for the 1956-62 year classes are found in Table 4 and compared in Figure 11. Only samples taken off the Washington coast were used so that successive year classes could be compared while minimizing any spatial effects. These growth curves generally fall into two sets. Individuals of the 1956-59 year classes were considerably larger at age than the members of the 1961-64 year classes. The growth curve for the 1960 year class falls between the two sets.

TABLE 2.—Age composition (percentage) of male and female hake taken each year off Washington, 1965-69.

Age (years)	1965		1966		1967		1968		1969	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
2	—	—	0.1	—	0.1	0.1	—	—	—	—
3	—	—	0.1	0.1	1.4	1.2	—	—	—	—
4	13.0	22.5	0.3	0.3	1.6	2.6	1.4	2.5	0.1	0.2
5	28.9	20.6	44.2	46.0	5.2	4.5	1.9	2.9	6.9	9.0
6	27.2	23.8	33.1	23.7	62.1	53.6	11.5	7.0	16.6	18.5
7	13.5	5.2	14.5	15.9	22.2	19.7	68.6	60.3	55.7	41.3
8	12.9	10.6	3.1	6.7	5.4	10.2	13.3	17.2	19.7	28.2
9	3.0	10.3	3.2	3.3	1.2	4.8	2.3	4.8	1.0	2.5
10	1.4	4.9	0.7	1.8	0.6	2.2	0.9	3.2	—	0.1
11	—	1.4	0.7	1.5	0.1	0.9	0.2	1.4	—	0.1
12	—	0.6	—	0.5	0.1	0.2	—	0.4	—	—
13	—	—	—	0.1	—	—	—	0.3	—	—
Sample size	1,474	2,196	1,355	1,724	1,195	1,432	1,047	1,546	1,009	811

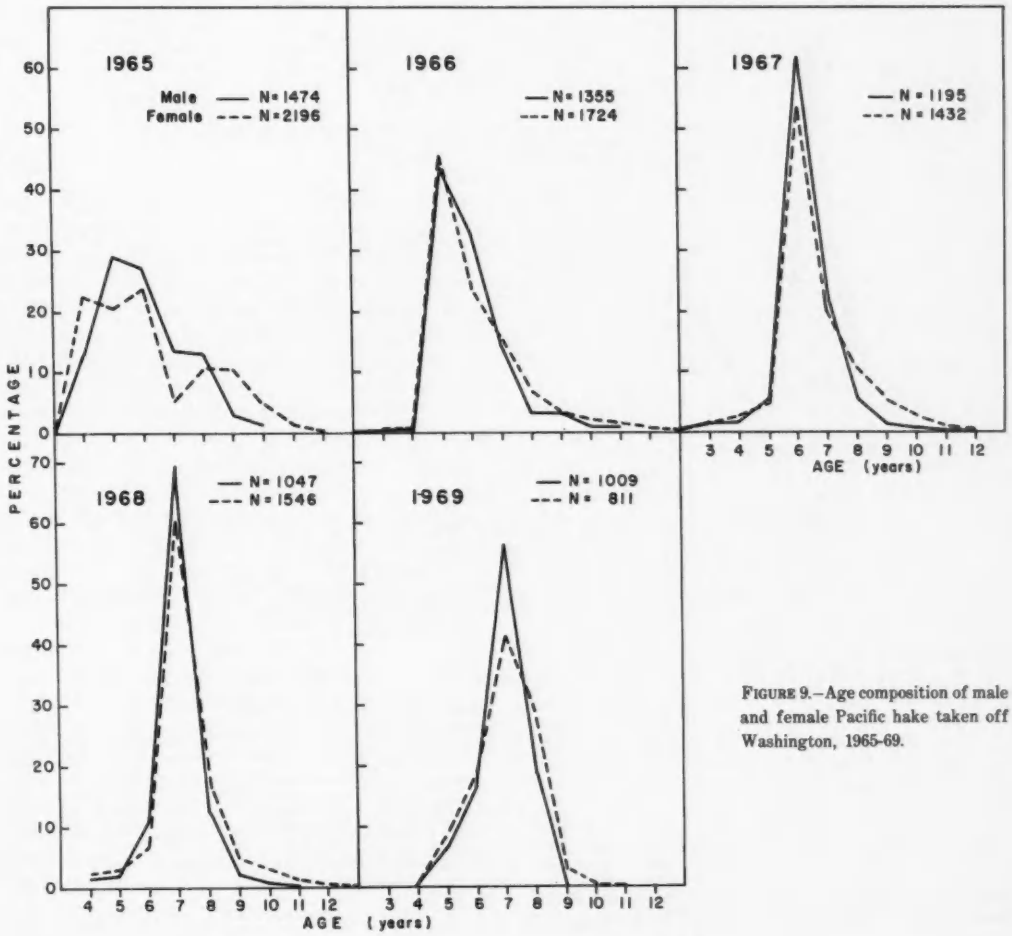


FIGURE 9.—Age composition of male and female Pacific hake taken off Washington, 1965-69.

TABLE 3.—Average body length at various ages for male and female hake taken off California, Oregon, and Washington during 1965-69.

Age (years)	Female		Male	
	Sample size	Mean length (cm)	Sample size	Mean length (cm)
1.0	385	[1]15.40	385	[1]15.40
2.0	36	28.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	—	—
13.3	6	61.83	—	—
	[2]4,453		[2]4,201	

[1]Assigned value based on the mean of all 1-yr-old hake; sex determinations were not available for 1-yr-olds.
[2]Does not include the unsexed 1-yr-old group.

While there is little variation apparent within year class groups, length at age may vary by as much as 4 cm between year class groups.

These data suggest that some variation in growth can occur among year classes, but the irregular sampling of all ages, particularly the youngest, precludes construction of complete growth curves by year class using length-at-age data. Therefore a back-calculation technique was utilized to reconstruct the growth curves for several year classes as a means of further examining year-class variation.

Back calculation of body lengths was based on an otolith radius-body length relationship derived from hake samples collected in 1966-68. Approximately 10 otoliths (5 male and 5 female) per 1-cm body length interval were selected for

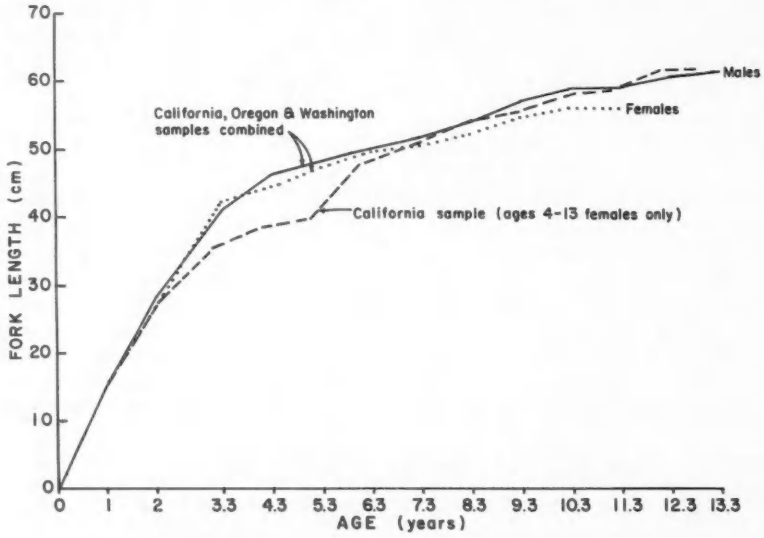


FIGURE 10.—Average fork lengths at various ages for Pacific hake collected off California, Oregon, and Washington combined, and from California alone (Best 1963).

TABLE 4.—Mean body length (cm) at various ages (in years) for 1956-62 year classes of hake.

1956		1957		1958		1959		1960		1961		1962	
Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length
—	—	—	—	—	—	—	—	—	—	—	—	3.0	35.6
—	—	—	—	—	—	—	—	—	—	4.3	44.9	4.5	47.8
—	—	—	—	—	—	5.7	52.5	5.3	48.9	5.5	48.2	5.3	48.7
—	—	—	—	6.7	53.9	6.3	52.6	6.5	51.6	6.3	49.2	6.3	49.7
—	—	7.7	54.2	7.3	53.9	7.5	54.8	7.3	53.2	7.3	50.6	7.5	50.6
8.7	54.9	8.3	55.2	8.5	56.1	8.3	55.9	8.3	54.1	8.5	51.8	—	—
9.3	57.4	9.5	56.8	9.3	56.5	9.3	56.6	9.5	54.2	—	—	—	—
10.5	57.8	10.3	59.7	10.3	58.2	10.5	57.0	—	—	—	—	—	—
11.3	58.7	11.3	58.0	11.5	60.0	—	—	—	—	—	—	—	—
12.3	60.0	—	—	—	—	—	—	—	—	—	—	—	—

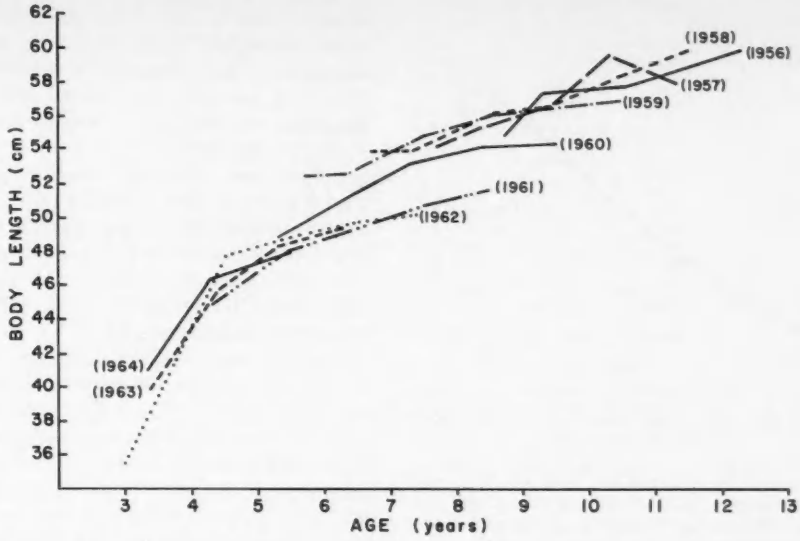


FIGURE 11.–Average fork lengths at various ages by year class (in parentheses) for Pacific hake taken off Washington, 1964-69.

analysis. A sample of 10 was not attained in those centimeter groups near the extremes of the length distribution nor in those length groups where 10 samples were taken but not all otoliths were readable. Fork lengths represented ranged from 11 to 68 cm. To facilitate the measuring all otoliths were photographed and enlargements made so that the prints were 16 times the size of the otoliths. Measurements were taken directly from each print. A midpoint was determined on the photograph of each otolith by measuring the distance from the anterior edge to the posterior edge of the first translucent zone and halving that measurement (Figure 12). Measurements were made from this midpoint to the anterior margin of each annulus and to the anterior edge of the otolith. When annuli were not clearly defined, measurements were not made.

The mean body length per centimeter of otolith radius was computed and plotted in Figure 13. A curve constructed from the individual observations (n = 370) is superimposed on the means. The curve was constructed from a third degree polynomial equation of the form $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$, where Y = estimated body length and X = otolith radius. This equation provided the best fit (smallest residual sum of squares and mean square) of the several functions examined (Table 5). The correlation

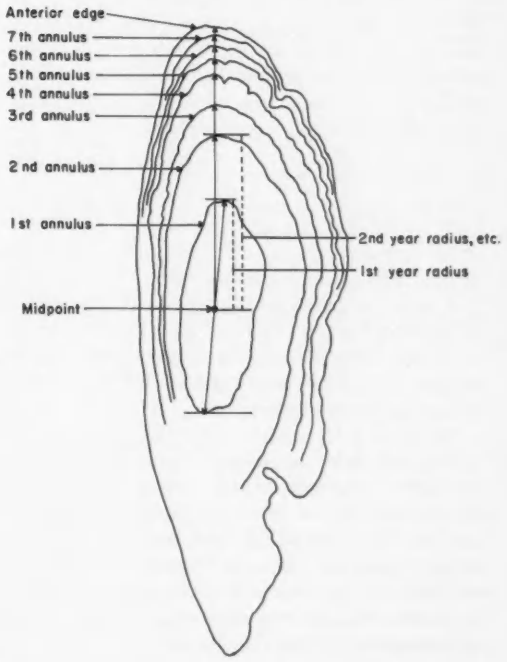


FIGURE 12.–Pacific hake otolith showing the calculated midpoint and measurement intervals from the midpoint to the anterior margins of successive annuli.

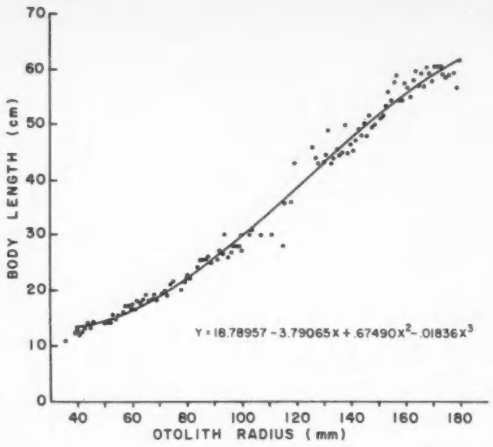


FIGURE 13.—A scattergram of mean body lengths per millimeter of otolith radius (as taken from a 16× photographic enlargement) and superimposed curve of the function used to back-calculate growth.

TABLE 5.—Functions examined for the best fit of otolith radius–body length data, corresponding residual sums of squares, and mean squares.

Function	Residual sum of squares	Mean square
$y = a + bx$	3,865	10.44
$y = a + bx + cx^2$	3,700	10.03
$y = a + bx + cx^2 + dx^3$	3,146	8.55
$y = ab^x$	7,611	20.57
$y = a^a x^b$	3,768	10.18

between estimated and observed values is 0.9860, so an improved fit was not attempted. The Y intercept is at 18.78957 cm indicating that the function does not adequately represent the otolith radius-body length relationship in fish less than 1 yr of age. Therefore the back calculation of body lengths beyond the range of the data fitted is obviously not meaningful.

The mean total otolith radii by age were used to back calculate lengths at age which are presented in Table 6 and compared in Figure 14 with observed lengths at age from combined 1965-69 samples. The atypical 1961 year class was excluded in this comparison. In spite of a certain amount of variation in the back-calculated curve (probably induced by the small sample size), the two curves correspond very well.

The lengths-at-age for five year classes (1957-61) were compared by back calculating the lengths of approximately equal numbers of males and females from each year class. Because there is some evidence in Table 7 that the radii of the first one or two annual marks increase as the total age increases, only otoliths from 7-yr-olds were used to avoid any possible age-related effects. Older specimens could not be used because they were not available in sufficient numbers and younger specimens had a growth history which was too brief. Fifteen otoliths of each sex for each of the 5 yr were selected. The desired sample size (30 per year class) was seldom obtained because many of the otoliths had deteriorated in storage so that opaque and hyaline zones could not be distinguished on the photographs.

Back-calculated lengths are presented in Table 8, and a comparison of back-calculated growth curves for the five year classes is made in Figure 15. It appears that year class variation was not great among the 1957-60 year classes, but that the members of the 1961 year class were on the average noticeably smaller at age than members of the other year classes. This latter observation

TABLE 6.—Mean otolith radii and back-calculated body lengths at various ages for Pacific hake.

Age (years)	Mean otolith radii (cm)	Calculated body lengths (cm)
1	6.08	16.57
2	9.06	26.19
3	12.53	41.13
4	13.50	45.44
5	13.60	45.88
6	14.43	49.45
7	14.80	51.00
8	16.44	57.30
9	15.79	54.92
10	17.29	60.11
11	17.74	61.44
12	18.30	62.92
13	17.90	61.86

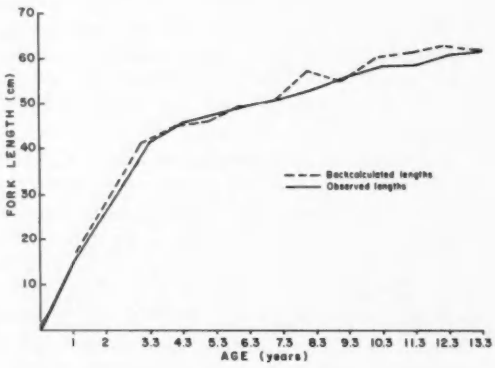


FIGURE 14.—A comparison of growth curves as constructed from observed and backcalculated fork lengths at various ages.

TABLE 7.—Mean radii (cm) of photographed otolith annuli by total age group.

Total age (years)	Annuli												
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th
1	5.96	–	–	–	–	–	–	–	–	–	–	–	–
2	5.85	8.87	–	–	–	–	–	–	–	–	–	–	–
3	7.10	10.13	12.53	–	–	–	–	–	–	–	–	–	–
4	6.34	9.73	11.66	13.13	–	–	–	–	–	–	–	–	–
5	6.57	10.03	11.50	12.87	13.57	–	–	–	–	–	–	–	–
6	6.38	9.73	11.51	12.79	13.79	14.32	–	–	–	–	–	–	–
7	6.16	9.59	11.60	12.97	13.89	14.37	14.71	–	–	–	–	–	–
8	6.18	9.86	12.02	13.63	14.90	15.61	16.15	16.50	–	–	–	–	–
9	6.33	9.80	11.56	12.89	14.05	14.53	14.94	15.39	15.66	–	–	–	–
10	6.44	9.92	11.65	13.39	14.57	15.66	16.21	16.73	17.14	17.50	–	–	–
11	6.60	9.84	11.38	13.08	14.42	15.52	16.00	16.54	16.94	17.36	17.66	–	–
12	6.75	10.85	12.75	14.50	15.50	16.10	16.60	17.60	17.90	18.10	18.40	18.60	–
13	7.15	10.45	12.20	13.40	14.35	14.95	15.35	15.75	16.20	16.55	16.90	17.25	17.65

TABLE 8.—Back-calculated body length (cm) at various ages for the 1957-61 year classes of Pacific hake.

Age (years)	Year class and (in parentheses) sample size				
	1957 (27)	1958 (15)	1959 (22)	1960 (27)	1961 (30)
1	19.02	18.64	16.45	16.85	16.95
2	31.16	31.01	30.36	29.92	28.50
3	38.71	39.05	38.65	37.11	37.06
4	44.61	40.66	46.09	46.12	43.58
5	49.31	50.14	50.92	50.38	47.60
6	52.28	50.98	53.74	52.65	49.88
7	54.10	54.61	55.51	54.20	51.48

corroborates the slow growth rate of the 1961 year class suggested by the length-age data presented previously. The 1961 year class was an extremely large year class numerically, exceeding by far the size of other year classes of record. Perhaps density-dependent growth was operative in this instance. The size of the 1961 year class may have been so large that the competition for food and space noticeably restricted the growth of individuals. It cannot be ascertained whether the members of smaller year classes might undergo density-dependent growth to a lesser extent or if the phenomenon is triggered only by unusually large year classes.

The von Bertalanffy growth equation is commonly used to describe asymptotic growth. It is used herein because it fits the data well and is readily incorporated in certain yield models. Von Bertalanffy's equation is $l_t = l\infty\, 1\text{-}e^{-k\,(t\text{-}t_0)}$, where l_t = body length at time t; $l\infty$ = estimated average maximum body length; k = rate of growth; t_0 = theoretical age when growth conforms to the von Bertalanffy equation. Since sexual differences in growth characteristics exist in Pacific hake, separate curves were fitted to male and female length data. Average length at age data from Table 3 were used to compute the growth curves. In this instance the growth of the 1961 year class was considered atypical and it was excluded from the analysis. A computer program[1] utilizing the method of Stevens (1951) was used to compute the constants for the von Bertalanffy equation. The resulting equations are: $l_t = 56.29\,(1\text{-}e^{-0.39\,(t\text{-}0.20)})$ for males and $l_t = 61.23\,(1\text{-}e^{-0.30\,(t\text{-}0.01)})$ for females. By comparison, Tillman's (1968) estimates of k were 0.41 for males and 0.19 for females. He reported that treatment of Best's (1963) data also yielded 0.19 for females. In the present study $l\infty$ for both sexes are reasonable estimates of average maximum body lengths. Males as long as 66 cm and females as long as 80 cm have been observed. Growth of Pacific hake is adequately represented by the von Bertalanffy equations as the curves fit the observed lengths-at-age very well (Figure 16). The curves are nearly superimposed until about age 5 when they begin to diverge and continue to do so with age. Although sex-specific growth rates are apparent, the growth rate of the entire Pacific hake population may be best represented by an equation based on data with the sexes combined. The growth equation with sexes combined is $l_t = 60.85\,(1\text{-}e^{-0.30\,(t\text{-}0.03)})$.

Growth in Weight

In 1964-69 length and weight data were collected on 2,417 male and 3,117 female Pacific hake taken from Washington to southern California. Lengths and weights were taken from fresh fish as they were unloaded from vessels at the processing plant and from research samples at sea. Fork lengths were taken to the nearest centimeter and weights to the nearest decagram. The majority of

[1]Program developed by George Hirschhorn, Northwest Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash.

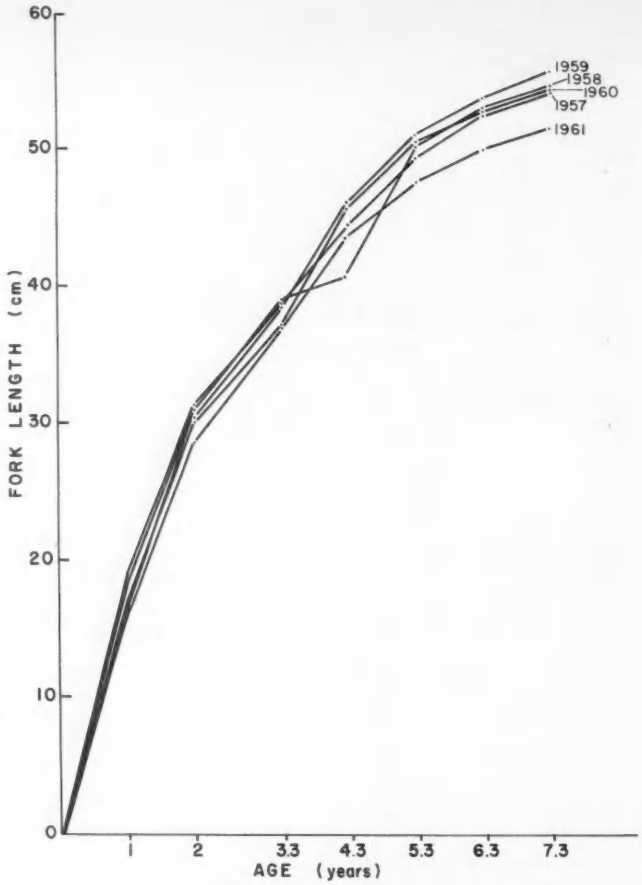
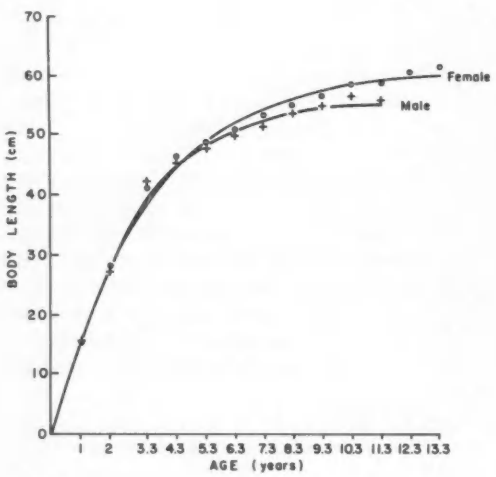


FIGURE 15.—Back-calculated growth curves for 1957-61 year classes. (Only otoliths from 7-yr-old specimens were used.)



observations were made from mature specimens in commercial samples, and therefore hake less than about 40 cm long were inadequately represented or not represented at all. The commercial data were fitted using the length-weight equation $W = aL^b$, where W = weight in grams, L = length in centimeters, and a and b are constants. In linear form this equation becomes $\log W = \log a + b (\log L)$. The length-weight relationships were calculated to be $\log W = -1.45990 + 2.55618 \log L$ for males and $\log W = -1.68944 + 2.69509 \log L$ for females (Figure 17).

Typically the exponent in the length-weight equation for most fusiform fishes approximates 3, implying isometric growth. On the basis of data

FIGURE 16.—Von Bertalanffy growth curves for male and female Pacific hake superimposed on mean body lengths at various ages. (o = females; + = males.)

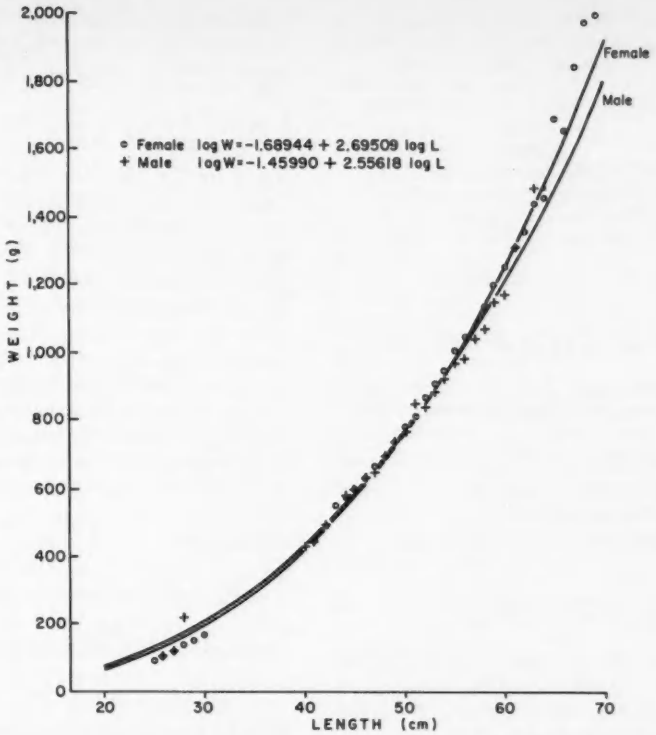


FIGURE 17.—Length-weight curves for male and female Pacific hake superimposed on mean body weights ($n \geq 5$).

from 58 female hake from California ports, Best (1963) estimated the exponent of the length-weight equation to be 3.0668. On the chance that the hake in commercial samples had lost weight between capture and delivery through the loss of body fluids, another pair of equations was fit to less extensive length-weight data taken aboard research vessels off Washington from freshly caught specimens. Student's t-test was used to test the null hypothesis that regression slopes calculated from research and commercial samples did not differ significantly from 3. All tests were significant at the 1% level (Table 9) and the hypothesis was rejected. A possible explanation is that because most specimens are in an immediate postspawning state as they arrive off Washington and Oregon, their weight relative to their length is less than it might be later in the year.

Growth in weight for males and females was calculated from the length-weight equations (Figure 18). These curves suggest that Pacific hake gain weight at an increasing rate until they are 3 yr old. After age 3 the rate of growth in weight decreases and remains roughly constant until death. By age 3, males have grown to approximately 50% of their total weight at 11 yr of age, whereas females by age 3 have attained about 40% of their total weight at 11 yr of age. The growth rates are sex specific and the curves begin to diverge noticeably between ages 3 and 4. At 11 yr of age females weigh on the average about 200 g

TABLE 9.—Results of t-tests to determine if slopes of length-weight regressions calculated from commercial and research samples differ significantly from 3. All comparisons were significant at the 1% level.

Sample type	Sum of deviations from mean (Σx^2)	Variance (Sxy^2)	Slope (b)	Sample size (n)	t
Commercial:					
Male	6.4084	0.0049	2.55618	2,417	16.02
Female	10.5651	0.0032	2.69509	3,117	17.62
Research:					
Male	2.6224	0.0154	2.63189	432	4.80
Female	4.2177	0.0075	2.65436	587	8.20

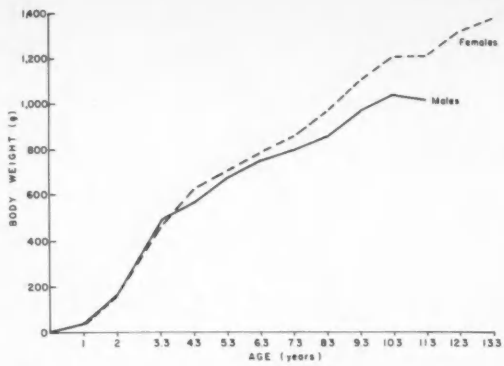


FIGURE 18.—Average body weight at various ages for Pacific hake collected off California, Oregon, and Washington, 1965-69.

more than males. For each sex, Table 10 gives average weight at age values, annual growth rates, and annual instantaneous growth rates, assuming exponential growth in weight.

SUMMARY AND CONCLUSIONS

Biological data from samples of Pacific hake taken in 1964-69 off the coasts of Washington, Oregon, and California were utilized to study the age and growth of the species.

TABLE 10.—Mean weight, annual increase in weight, and instantaneous growth rate at various ages for male and female hake taken off California, Oregon, and Washington, 1964-69.

	Male			Female		
Age (years)	Body weight (g)	Annual increase (%)	Instant. growth rate	Body weight (g)	Annual increase (%)	Instant. growth rate
1	37.6			32.4		
		318	1.43		400	1.61
2	157.0			162.9		
		216	1.15		183	1.04
3.3	496.0			459.5		
		15	0.14		36	0.31
4.3	570.0			626.5		
		18	0.17		13	0.12
5.3	674.6			703.5		
		12	0.11		12	0.11
6.3	751.0			786.2		
		6	0.06		8	0.08
7.3	798.2			853.6		
		7	0.07		13	0.12
8.3	856.8			966.8		
		13	0.12		14	0.13
9.3	964.1			1,102.5		
		8	0.08		9	0.09
10.3	1,040.6			1,207.2		
		0	0.00		0.3	0.00
11.3	1,014.8			1,211.1		
		—	—		8	0.08
12.3	—			1,319.6		
		—	—		4	0.04
13.3	—			1,374.0		
		—	—		—	—

The method of age determination from annuli on otoliths was examined, and all evidence suggests that the method provided reliable age data.

Several sources of variation in the age structure of the population were considered. The relative size of newly recruited year classes varied substantially, creating noticeably annual variation in the age composition. There was no detectable seasonal variation in the age composition of the hake population found off Washington from spring through fall. Latitudinal stratification of hake by age (known to occur over large geographical areas) was further examined, and some variation in age composition was found even among ½ degree intervals of latitude off the Washington coast. The relative abundance of the 4- and 5-yr-olds decreased as sampling progressed northward from the mouth of the Columbia River to the Strait of Juan de Fuca, while the relative abundance of 7- to 10-yr-olds increased. This stratification of ages by latitude supports the theory that there is a northward migration of hake in the early spring along the Pacific coast of North America with the older (larger) individuals tending to migrate farthest. There is little variation in age composition due to sex, except that the longer lived females tend to predominate from 8 to 10 yr of age and are usually the sole survivors at 11-13 yr of age.

Pacific hake grow rapidly in length during their first 3 yr after which growth slows and becomes asymptotic. At about 4 yr of age, females grow noticeably faster and by age 11 may average 3.12 cm longer than males. Individual males may reach 66 cm, while some females may reach 80 cm in length. Year class variation in growth rates was detected by analysis of age-length data and back calculation of growth from otoliths. The equation $Y = 18.78957 - 3.79065X + 0.67490X^2 - 0.01836X^3$ was used to describe the relationship of body length (Y) and otolith radius (X).

The extraordinarily large 1961 year class grew at a substantially slower rate than the 1957-60 year classes. This difference possibly is indicative of density-dependent growth. Growth in length can be expressed adequately by the von Bertalanffy growth equations:

$l_t = 56.29\,(1-e^{-0.39\,(t\,-0.20)})$ for males,
$l_t = 61.23\,(1-e^{-0.30\,(t\,-0.01)})$ for females, and
$l_t = 60.85\,(1-e^{-0.30\,(t\,-0.03)})$ for the sexes combined.

Growth in weight was determined by applying the length-weight equations:

$\log W = -1.45990 + 2.55618 \log L$ for males, and
$\log W = -1.68944 + 2.69509 \log L$ for females

to average length-at-age data. By age 3, males have grown to about 50% of their total weight at age 11, and females to about 40% of their total weight at age 11. At 11 yr of age females weigh on the average 200 g more than males. Males attain an average weight of about 1,015 g by age 11 and females reach an average weight of 1,374 g by 13 yr of age.

ACKNOWLEDGMENTS

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EVALUATION OF THE RETURN OF ADULT CHINOOK SALMON TO THE ABERNATHY INCUBATION CHANNEL

ALLAN E. THOMAS[1]

ABSTRACT

Adult returns of progeny of the 1964 year class of chinook salmon, *Oncorhynchus tshawytscha*, were determined for the Abernathy incubation channel, natural production, and hatchery sources. A total of 4,620,600 fry were released from the channel into Abernathy Creek (state of Washington) as unmarked fry. Natural production in the creek was estimated from spawning ground counts and fyke net sampling of migrants at 16,700 fry, or 0.36% of the total unmarked fish. A total of 557,649 hatchery fish were marked by feeding tetracycline, and 161,579 were both fin-clipped and fed tetracycline. All 2-, 3-, and 4-yr-old adult fish returning to the hatchery holding pond were examined for fin clips and fluorescent bands on the vertebrae. Returns from hatchery sources were 506 fish or 0.070%. Potential egg production was 865,000, or 76% of the original 1,142,604 eggs. Returns from the channel totaled 733 fish or 0.016%. Egg potential was 2,050,000, or 35% of the original 5,888,048 eggs. Returns attributed to Abernathy Creek totaled only three fish and egg potential was 0.2% of the original 2,880,000 eggs. Survival of this year class was considerably below the 9-yr average of 0.118%. Intuitively, costs favor incubation channel production over hatchery production. However, additional studies are needed to determine if contributions to the fisheries and survivals are comparable in years of better year class survival.

Spawning and incubation channels for salmon produce higher survivals of downstream migrants than do natural spawning grounds. Studies by Gangmark and Broad (1956), Lister and Walker (1966), Thomas and Shelton (1968), and others have shown that channels with flow and sediment control devices can produce many times as many migrant-sized fish as are produced by the parent stream. Little information is available on the percentage of fry produced in channels that return as adults. Such data are needed to determine the value of incubation channels for supporting and maintaining salmon runs.

In the present study, I compare the survival to the adult stage of chinook salmon, *Oncorhynchus tshawytscha*, from three sources: the Abernathy incubation channel (near Longview, Wash.); the Salmon-Cultural Laboratory hatchery adjacent to the channel; and natural spawning in Abernathy Creek.

MATERIALS AND METHODS

Problems were encountered in selecting the techniques to use to distinguish returning adults from the various sources. Fin-clipping presented two problems. First, fin-clipping of fry produced in the channel was undesirable mainly because of the small size of the fry (average weight, <0.5 g). The chance of injury or incomplete removal of fins would be high. Fin-clipping of hatchery fish has been shown to reduce adult returns by 43.3% (Weber and Wahle 1969). Second, the daily numbers of fry migrating varied widely (from a few thousand to over 120,000), depending upon water conditions. Fin-clipping at a practical rate would require that many fish be held beyond their normal migration date.

Marking channel and creek migrants with tetracycline would not be acceptable. Although marking fish in this manner using techniques developed by Weber and Ridgway (1962) had no detrimental effect on adult survival (Weber and Wahle 1969), the drug is normally administered in the food. The artificial feeding of channel fish might alter their characteristics and invalidate the survival evaluations. Attempts to mark small fish by immersion in solutions of tetracycline and 4% dimethyl sulfoxide have shown some favorable results (Richard C. Johnsen, pers. commun.), but the technique has not been sufficiently developed for reliable, large-scale marking.

For these reasons migrant fry from the incubation channel and Abernathy Creek were not

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marked. Rather, the numbers migrating downstream were determined and the returns were compared with returns from marked hatchery fish stocked in the creek. It is assumed that fish migrating from the channel and Abernathy Creek would have the same rates of survival. Table 1 summarizes the number, size, time of migration, and mark of each of the fish sources involved in the evaluation.

TABLE 1.–Summary of the number, size, time of migration, and mark of the various fish sources included in the evaluation.

Origin of migrants	Number	Size (g/fish)	Time of migration	Mark
Abernathy Creek	16,700	[1]0.5	[1]11/64-4/65	none
Incubation channel	4,620,600	0.5	12/64-4/65	none
Hatchery	61,000	8.2	5/65	2-OTC[2]
	445,500	4.8	5/65	2-OTC
	51,149	16.8	8/65	3-OTC
	161,579	16.8	8/65	3-OTC + fin clips

[1]Approximate size and time of migration based upon fyke net sampling.
[2]Oxytetracycline.

Migrants from the Incubation Channel

A total of 4,620,600 unmarked fry were released from the channel during the 1964-65 season. This number represents a 78.5% survival from the 5,888,100 eyed eggs planted. If the mortality of green eggs is also considered, the survival to migrant stage was 75.0%. A description of techniques for planting eggs and counting fry was given by Thomas and Shelton (1968).

Migrants from Abernathy Creek

Numbers of female chinook salmon which spawned in Abernathy Creek during the 1964 spawning season were estimated at 576 from spawning ground counts. On the basis of an average of 5,000 eggs per female, an estimated 2,880,000 eggs were deposited in the creek. Fry migrating downstream from this area were sampled with a fyke net, a method demonstrated to be reliable by Tait et al (1962). Recaptures from known numbers of marked fish released upstream indicated that the net sampled 13.3% of the migrating fish; the calculated survival of migrants from natural spawning was 16,700, or 0.58%. Flooding and superimposition of eggs during spawning are probably responsible for this low survival. These fish were unmarked and returning adults could not be distinguished from those which originated in the incubation channel.

Chinook salmon spawning area in Abernathy Creek extends for about 1 mile below the hatchery weir. Returns from natural spawners would not necessarily enter the hatchery holding pond.

Releases of Hatchery Fingerlings

All fish released from the Salmon-Cultural Laboratory hatchery were marked in some manner for later identification. Initially, all fish were marked in mid-April 1965 by feeding tetracycline after the technique developed by Weber and Ridgway (1962). All fish in a 100-fish sample examined in late April showed fluorescent bands on their vertebrae. Fish released into Abernathy Creek in May had two bands and those in August, three bands. These second and third marks were poor because the fish fed little, presumably because of the high level of drugs in the diet. Total hatchery fish released with only tetracycline marking totaled 557,649.

Two groups of fish used in a nutrition experiment received double fin clips, in addition to the tetracycline marks. These two groups served as controls in that the returning adults would be easily recognizable from the clipped fins, and a check of their vertebrae would indicate the persistence of the fluorescence. The fin-clipped groups, which numbered 161,579, were released in mid-August 1965.

Treatment of Adult Fish

All adult chinook salmon returning to the holding pond at the Salmon-Cultural Laboratory were examined during 1966-68. All fish returning as 2-yr-old jack salmon and as 3- and 4-yr-old adults were examined. Past records of age classification indicated that numbers of 5- and 6-yr-old adults in the Abernathy Creek spawning run are insignificant. Fish that returned to Abernathy Creek but not to the hatchery holding pond were not included in the evaluations. No attempt was made to sample the sport or commercial fisheries or to search the adjacent streams and hatcheries for strays. The evaluation is based only upon returns to the Salmon-Cultural Laboratory holding pond. No correction was made for strays from other hatcheries or streams that might enter the holding pond and be counted as survivors from the channel since their number would be insignificant (Worlund et al. 1969).

All adult fish were measured and the sex was

recorded. Scales were taken for age determination. Age determinations of fish returning to the hatchery in previous years had indicated the size range for 2-yr-old jack salmon, but 3- and 4-yr-old fish could not be separated by size. During the 1966 spawning season, a vertebra was removed from all fish smaller than the maximum length previously found for 2-yr-old fish, for determination of tetracycline marks. During the 1967 and 1968 spawning seasons, a vertebra was also removed from all fish in the size range of previous 3- and 4-yr-old fish.

Vertebrae were scanned under ultraviolet light by the technique described by Weber and Ridgway (1962). Vertebrae with tetracycline marks were classified as hatchery fish. The age of fish without vertebra marks was determined by examination of the scales. All unmarked fish of the correct age were considered to be recoveries from either the channel or creek. Tetracycline bands were visible in the vertebrae of all fin-clipped salmon.

Adult returns from two sources—the hatchery or Abernathy incubation channel and Abernathy Creek—were determined by measuring and aging fish and by identifying those with fin clips and tetracycline marks on vertabrae. Potential egg production was calculated on the basis of 5,000 eggs per female, the average number found in chinook salmon returning to the hatchery in previous years.

RESULTS

Adult Returns from Hatchery-Reared Fingerlings

Table 2 presents adult return data for both 1) the fin-clipped plus tetracycline-marked group and 2) the tetracycline-marked groups. Survival of fish that had been marked with both tetracycline and fin clip was low; of 161,579 fingerlings released, only 20 returned. Disease and parasite problems encountered during the summer rearing season probably contributed to the low survival. Fish released before the warm-water season appeared to have better survival. The total survival was 0.070%.

TABLE 2.—Number of male and female adult chinook salmon returns from 719,228[1] hatchery-reared fingerlings released from the Salmon-Cultural Laboratory hatchery, 1965.

Age at return (years)	Males	Females	Potential egg production (thousands)
2	209	0	0
3	90	96	480
4	34	77	385
Total	333	173	865

[1]Of this total, 557,649 fish were released with tetracycline bands and 161,579 with double fin clips and tetracycline bands.

Adult Returns from Abernathy Incubation Channel and Creek

The percentage returns of fish from the Abernathy incubation channel (0.016%) was considerably lower than that from the hatchery (Table 3). The higher ratio of female fish, however, resulted in a relatively higher number of eggs per returning fish.

The numbers of returning fish that originated in Abernathy Creek were insignificant. If the survival rate after migration is assumed to be identical for channel and creek migrants, only 0.36% of the 736 returning unmarked adults—or about 3 fish—were from the creek.

TABLE 3.—Number of male and female adult chinook salmon returns from 4,620,600 fry released at the Abernathy incubation channel, 1965.

Age at return (years)	Males	Females	Potential egg production (thousands)
2	16	0	0
3	202	220	1,100
4	107	188	940
Total	325	408	2,040

DISCUSSION

Survival was low from chinook salmon of the 1964 year class released from most Columbia River hatcheries, as they were in this experiment. Reasons for the poor survival are largely unknown. Although the evaluation of survival from several year classes would have been desirable, comparisons of survival from the different sources of young fish provide information on the relative survival of channel-reared and hatchery-reared fish, as well as an insight into the potential survival from an incubation channel. Ideally, sufficient adults should return to a salmon hatchery to provide 100% or more of the original egg supply. Assuming about 5,000 eggs per female and a 50:50 ratio of males to females, a chinook hatchery is self-sustaining when the return is about 0.045%.

TABLE 4.—Potential egg production of adult chinook salmon returns in relation to original egg numbers from which they were produced.

Source of downstream migrants	Return of adult salmon		Salmon eggs		
			Original number (thousands)	Potential production from adults	
	Number	Percent		Number (thousands)	Percent of original number
Salmon-Cultural Laboratory hatchery	506	0.070	1,143	865	76
Abernathy incubation channel	773	0.016	5,888	2,040	35
Abernathy Creek	3	0.016	2,880	7	0.2

Potential egg replacement of adult returns from the various sources is shown in Table 4. The adult return from the hatchery totaled 0.070%; however, more than 40% of the adult fish returned as 2-yr-old males. Only about 76% of the original eggs were replaced for this brood year. Although the percentage survival of hatchery fish was more than four times that of channel fish, the advantage in egg replacement was less than twofold. Even so, a channel could not operate long with a less than 35% replacement of eggs. If adults from natural spawning are assumed to enter the holding pond at an equal ratio with those from the channel, possible egg replacement from the creek source was only about 7,000.

The return of chinook salmon as 2-, 3-, and 4-yr-old, and sometimes as 5- and 6-yr-old fish, ensures overlapping of brood stocks. Consequently returns from year classes with poor survival are mixed with returns from other year classes, to help ensure that the hatcheries and streams may still have adequate egg supplies.

Production of salmon by incubation channels is usually evaluated only by the number of outmigrants produced and the total number of adults that return. The origins and ages of adults are seldom investigated.

Only relative comparisons can be made of survival from channel and hatchery releases due to variables such as time of release, size at release, and nutritional background. The channel had the sizable advantages of having very low costs for rearing the fry and no cost for food.

A 9-yr average of adult returns to the hatchery was 0.118%. Survival to adults from the 1963 year class of fish released by the hatchery was about 0.39%. There were no major differences in fish diet, times of stocking, or other known factors that might improve survival of this year class over that of the 1964 year class. If it is assumed that survivals of fish from the channel follow the same trends as do those from the hatchery, the more than fivefold greater hatchery returns for the 1963 year class would be reflected in channel production returns. This would provide more than sufficient egg production replacement. However, additional studies are needed to confirm this survival assumption.

ACKNOWLEDGMENT

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ECOLOGICAL STUDIES OF THE PUERULUS LARVAL STAGE OF THE CALIFORNIA SPINY LOBSTER, *PANULIRUS INTERRUPTUS*[1]

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ABSTRACT

Ecological and related behavioral studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*, involved the development and use of artificial and natural seaweed habitat traps, special paired neuston nets, and underwater night-lights for collecting and observing pueruli in nature. The results obtained indicate that pueruli first enter the coastal waters off San Diego, Calif., during May, and continue to appear regularly through September, but with no apparent relationship to lunar or temperature cycles.

Pueruli exhibit a strong attraction to floating habitat traps containing the surfgrass *Phyllospadix torreyi* and to bright lights at night. The results also suggest that the puerulus is a surface-swimming, pelagic form which may actively seek out specific nearshore areas for settlement, and thereby serve the important function of returning larval stages to areas suitable for demersal life of the young juveniles.

Previous studies of the California spiny lobster, *Panulirus interruptus* (Randall), and other spiny lobster species have concentrated primarily on either the adult or phyllosoma larval stages, leaving the biology of the intermediate, yet very important, puerulus and juvenile stages relatively unknown. This is particularly true for *P. interruptus*. Prior to the present study, essentially nothing was known about the ecological requirements or behavior of the puerulus or early juvenile stages, which together represent a period of 2-3 yr in the life history of this species. This is an unfortunate situation for an animal as heavily exploited by a commercial fishery as the California spiny lobster because, as Thorson (1950) has indicated, the abundance of any adult population is primarily dependent on the recruitment, survival, and growth of its larval and juvenile stages. Consequently, attempts to improve fishery yields through a better understanding of adult behavior and population ecology alone provide only a partial and temporary solution to the problem.

Increasing fishing pressure on the steadily declining stocks of *P. interruptus* and other spiny lobster species urges more than an academic interest in the ecological requirements of their puerulus and juvenile stages. On the basis of this information, for example, it may be possible to protect their natural habitats or to develop supplementary artificial habitats for them in nature. Techniques for culturing these stages under artificial conditions, as a means of supplementing natural stocks, must also be given serious consideration for the following reasons.

Evidence concerning *P. interruptus* (Johnson 1956, 1960, 1971) and other palinurid species (see, for example, Chittleborough and Thomas 1969) suggests that a majority of the phyllosoma and puerulus larvae may be lost from the population due to their long larval life (5-10 mo), during which they may be swept hundreds of kilometers offshore. Because of their small size, the surviving postpuerulus and early juvenile stages probably experience much higher predation mortality rates than do the adults (Winget 1968). In addition, evidence from limited studies of other spiny lobster species, including *P. argus*, *P. longipes cygnus*, and *Jasus edwardsii*, suggests that the nursery grounds of their postpuerulus and early juvenile stages are located in protected bays or estuaries (Sheard 1949; Lewis et al. 1952; Witham et al. 1964, 1968; Sweat 1968; C. B. Kensler, pers. commun.). If such estuarine nursery grounds are required by the early benthic stages of *P. interruptus*, reduction of this type of natural habitat as the result of commercial developments and water pollution may create a "weak link" in the life history of this species, at least within part of its geographical range.

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Aquaculture of *P. interruptus* or other palinurid lobsters, starting with the egg, has been attempted by several investigators as a means of bypassing what appears to be an inefficient recruitment process in nature. Yet all attempts to culture the phyllosoma larval stages from the egg through to the puerulus stage have been unsuccessful (for example, see Dexter 1972). This approach does not appear to be feasible at the present time, particularly on a mass culture basis, due to the long duration (5-10 mo in nature) and the poorly understood requirements of the delicate phyllosoma larval stages. In contrast, the succeeding puerulus and juvenile stages of spiny lobsters respond well to laboratory culture (Kensler 1967; Witham et al. 1968; Serfling and Ford in press a, b). Thus, if the puerulus stage of *P. Interruptus* proves to be abundant and relatively easy to collect in large numbers, particularly in certain offshore waters where these individuals might otherwise be swept away from coastal nursery grounds, it may be advantageous to supplement natural stocks by collecting pueruli and holding them in mass culture under controlled, optimal conditions through at least the early juvenile stages. These pueruli could either be reared directly to a marketable size under artificial conditions, or returned to the ocean, after passing the potentially critical early juvenile stages, for final growth and maturation. This approach to spiny lobster culture has also been proposed for *P. argus* by Ingle and Witham (1969).

The lack of ecological information on the puerulus stage of any spiny lobster species is due largely to the fact that investigators usually have been unable to collect more than a few individuals, despite extensive sampling in areas where they might be expected to occur. Consequently, the central question precluding further research has concerned the mode of life of the puerulus stage, i.e., whether it is primarily a benthic or pelagic form.

Evidence presented in the literature thus far supports about equally each side of the issue. Investigators who have failed to collect more than a few isolated pueruli, even after years of extensive sampling by conventional methods (Lewis et al. 1952; Johnson 1956, 1960, 1971; Harada 1957; Saisho 1966; Sims and Ingle 1966; Lazarus 1967), have concluded that the puerulus stage of their respective species is either primarily benthic, or concentrated in unknown pelagic areas. On the other hand, Gurney (1942), Sheard (1949), George and Cawthorn (1962), Chittleborough and Thomas (1969), and Chittleborough (1970) were able to collect small numbers of individuals in net hauls far out to sea, and thus suggested that the puerulus is a free-swimming stage.

Harada (1957) and Johnson (1960) reported collecting a few pueruli which were attracted to bright lights over shallow water at night, but both authors apparently believed they were lured from the bottom. Yet Lindberg (1955) reported that University of Hawaii personnel collected several pueruli of a *Panulirus* species which were attracted to surface night-lights in water several hundred meters deep, thereby eliminating the possibility that they were attracted from the bottom. Witham et al. (1968), Sweat (1968), Phillips (1972), and we have successfully attracted large numbers of pueruli to artificial habitat traps floating at the surface, thereby offering the first strong evidence that the puerulus is primarily a pelagic, surface-dwelling form.

Preliminary observations made originally by J. C. Van Olst (pers. commun.) in the spring of 1968, demonstrated that puerulus larvae of *P. interruptus* occurring in local coastal waters could be attracted to bright lights suspended underwater near the surface at night. This discovery prompted the following investigation into several aspects of puerulus behavior and ecology. The specific objectives of this study were: 1) to determine the mode of life of the puerulus stage of this species, e.g., whether it is primarily benthic or pelagic; and, having done so, 2) to develop and apply suitable field sampling techniques to study the general dynamics of puerulus recruitment with regard to seasonal, lunar, and daily periodicity, area of settlement, specific habitat preferences, and migratory behavior; and 3) to estimate the general abundance and possibility of collecting large numbers of this stage for use in aquaculture. Closely related studies were also conducted concurrently to investigate the habitat preferences and the natural growth rates of the early juvenile stages in nature, as well as the growth and survival of the juvenile stages at elevated temperatures in recirculating culture systems (Serfling 1972; Serfling and Ford in press a, b).

MATERIALS AND METHODS

The failure of standard sampling methods used by previous investigators to collect the puerulus

stage prompted the development of novel equipment and techniques. These included underwater night-lights of high intensity, floating artificial and natural seaweed habitat traps, and a special paired neuston net, which are described in the following sections.

Underwater Night-Lights

Most of the night-light observations and collections were made from an adjustable ladder platform near the end of the Scripps Institution pier, at the position shown in Figure 1, under a variety of environmental conditions. A standard motion picture projection lamp of either 500 or 1,000 W was waterproofed at the electrical connection with silicone sealant. The light was mounted on a pole and lowered 30-50 cm below the surface. This unit illuminated a spherical area 5-8 m in diameter, depending on water turbidity. When suspended in this way it provided much greater illumination than when suspended just above the surface. Pueruli attracted to the light were removed with a dip net and maintained alive for further studies.

Seaweed Habitat Traps

Pueruli placed in aquaria quickly settled and remained hidden in a variety of intertidal rock and plant substrates, but showed a preference for the surf grass *Phyllospadix torreyi*. They would continue to cling to any of these substrates, even when removed from the water. In an attempt to take advantage of this behavior, a variety of containers (Figure 2) for holding *Phyllospadix* and various species of red algae were floated under the lighted end of the Scripps Institution pier at the positions shown in Figure 1. The pier lights (three 200 W incandescent flood lamps mounted approximately 15 m above the water) apparently attracted pueruli to the pier, and the seaweed habitat traps provided convenient refuges in which they settled. The traps were retrieved and examined for pueruli every 4-6 days, providing a standard sampling system which could be operated continuously. The same types of habitat traps were also maintained on buoyed lines at several coastal locations in water 3-30 m deep, as discussed in a later section.

A variety of natural and artificial seaweed habitat trap designs, shown in Figure 2, were tested initially to develop a type most suitable for attracting pueruli. Included in the evaluation were

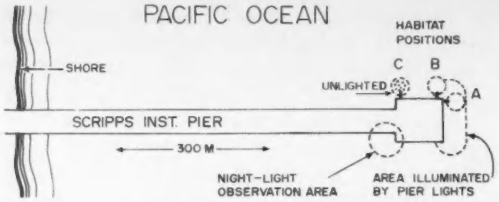

FIGURE 1.–Standard positions of puerulus habitat traps placed on the Scripps Institution pier, and the position from which night-light observations and collections of pueruli were made.

several models of the "Witham" habitat design used by Witham et al. (1968) for collecting *P. argus* pueruli (Figure 2C). This trap was constructed of a synthetic fibrous material labeled "Conservation Web #200," manufactured by Minnesota Manufacturing and Mining Company.[3] The traps we developed and tested consisted of wood frames which contained either synthetic materials, e.g., burlap, foam rubber, nylon mop, and plastic screen and netting, or fresh natural seaweeds, held within either plastic cage sides (Figure 2A, B), or within net bags or wire screen (Figure 2D, E).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

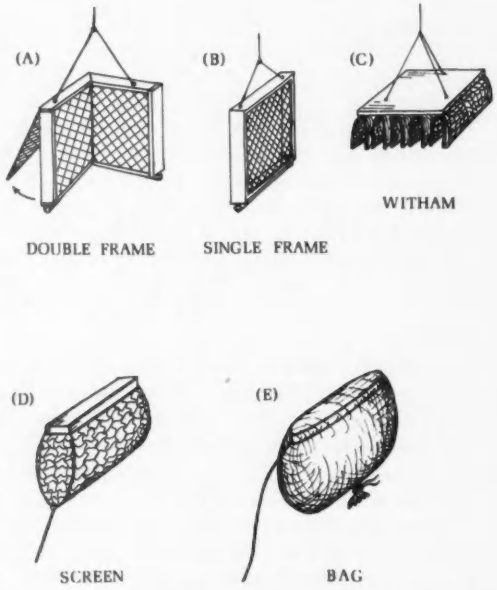

FIGURE 2.–Floating habitat trap designs employed in sampling puerulus larvae of *Panulirus interruptus*.

Suspension of the Habitat Traps

The strong surf and current conditions prevailing around the pier pilings required the development of a special system for suspending the habitat traps, as shown in Figure 3. This system allowed the trap to rise and fall during the tidal cycle, which has a vertical range of approximately 2.5 m, and in response to wave motion, thereby always remaining at the surface. The counterweight maintained a taut line and counteracted drag on the habitat trap caused by currents. No bottom anchor was necessary, thus eliminating problems of retrieval and fouling on kelp, and allowing the traps to be raised and lowered easily for examination. The traps also were held away from the pier pilings by the pole extension in order to prevent damage and entanglement.

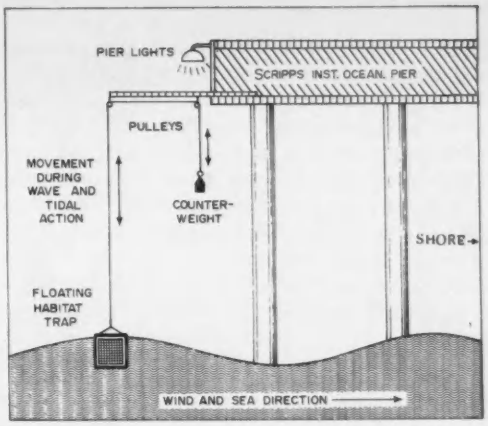

FIGURE 3.—The method employed in suspending habitat traps from the Scripps Institution pier.

Paired Neuston Nets

The results of night-lighting operations, discussed in a later section, suggested that the puerulus stage of *P. interruptus* swims within a few centimeters of the ocean surface. Thus, plankton or other nets towed below or near the surface probably would fail to catch this stage. Even surface tows made with a net breaking the surface might not be successful if it were trailed directly behind a vessel, because the "snow plow" action of the vessel might effectively push surface organisms away from the path of the net. Thus, paired neuston nets which could be mounted laterally on a small boat were developed to allow unobstructed surface water sampling, as shown in Figure 4. The presumed rarity of the puerulus stage required that these nets be of relatively large mesh size (5.0 mm) to allow reasonably fast towing speeds with a small boat (approximately 3 knots) and the filtration of large volumes of water. The short length and lateral position of the nets allowed their cod ends to be removed and emptied periodically without hauling the entire net from the water. The nets were towed with approximately 30% of the frontal area above water to ensure continual filtration of the top few centimeters of surface water, even during periods of low surface waves. The average frontal net area maintained submerged was approximately 0.7 square meter per net. Only rough estimates were made of the volumes and surface areas of water filtered during initial trials conducted during this study, as these were primarily concerned with evaluation of the sampler and with qualitative rather than quantitative results. The estimates of the water volume and surface area sampled were based on average boat speed and duration of the tow.

RESULTS

Night-Light Observations

Night-light observations were first conducted briefly in May 1968, and then resumed for a 2-mo period in September 1968. Night-light observations were also conducted again in the spring and summer of 1969, primarily to supplement information from the habitat traps also maintained during this period. The results of these observations, together with pertinent environmental data, are summarized in Table 1. During calm evenings in September 1968, pueruli were collected from the Scripps Institution pier at an average rate of approximately 4 per hour, with the highest rate reaching 12 pueruli collected within 90 min (8 per hour). No pueruli appeared during night-lighting conducted in October 1968, and further attempts were curtailed due to the onset of rough winter surf conditions which made the operation difficult. Night-lighting activities also were conducted at other San Diego localities during the period September-October 1968. These were: Quivira Basin in outer Mission Bay, Shelter Island in outer San Diego Bay, and the Imperial Beach pier. No pueruli were observed at any of these

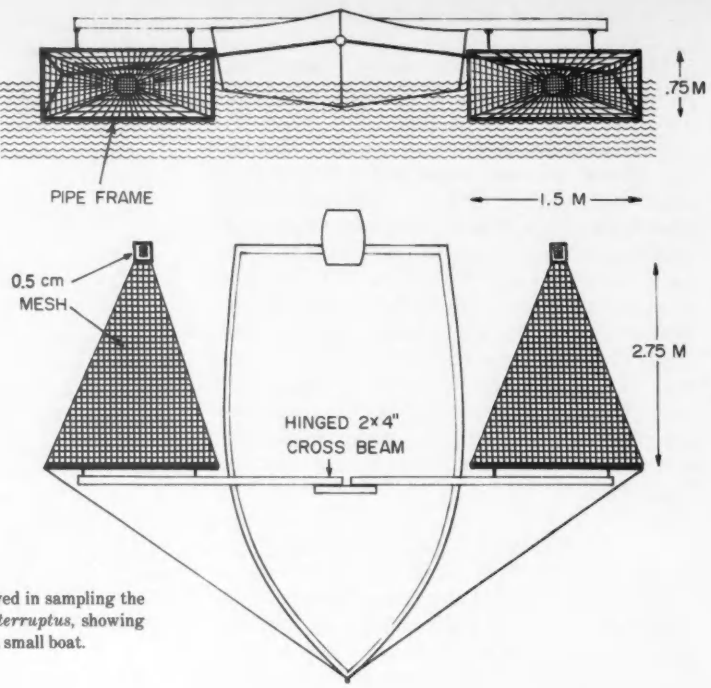

FIGURE 4.—Paired neuston nets employed in sampling the puerulus larval stage of *Panulirus interruptus*, showing the method used to deploy them from a small boat.

TABLE 1.—Results of night-light sampling for pueruli at the Scripps Institution pier and other San Diego localities.

Date	Number collected	Location	Time of sampling	Moon phase	Water temp. (°C)	Sampling period (min)	Suitability of conditions[1]
1968:							
May 15	0	Mission Bay	2000-2130	Full	16.0	45	Good
May 20	1	Scripps	2000-2130	Last Quarter	15.7	50	Fair
May 25	0	Mission Bay	1930-2030	New	16.4	60	Good
Aug. 28	9	Scripps	2130-2250	First Quarter	18.6	60	Good
Sept. 4	0	Imperial Beach	2030-2200	Full	20.7	80	Good
Sept. 7	4	Scripps	2200-2330	Full	20.0	40	Fair
Sept. 10	12	Scripps	2100-2230	Full—Last Quarter	20.5	90	Excellent
Sept. 16	3	Scripps	2000-2045	Last Quarter	20.7	40	Good
Sept. 26	4	Scripps	2000-2100	New—First Quarter	19.5	40	Fair
Oct. 2	0	Scripps	2230-2330	First Quarter—Full	18.3	50	Good
Oct. 10	0	Shelter Id.	2130-2250	Full—Last Quarter	18.5	80	Good
Oct. 20	0	Scripps	2200-2300	New	17.3	40	Good
Oct. 30	0	Scripps	2330-2430	First Quarter	16.8	30	Fair
1969:							
Apr. 5	0	Scripps	2030-2130	Full—Last Quarter	14.8	15	Poor
Apr. 20	0	Scripps	2130-2250	New—First Quarter	15.5	50	Good
May 7	0	Scripps	2030-2130	Last Quarter	15.9	20	Poor
May 15	0	Scripps	2130-2230	New	16.2	60	Good
May 23	6	Scripps	2145-2345	First Quarter	17.3	90	Good
June 4	3	Scripps	2200-2300	Last Quarter	18.1	30	Fair
July 10	14	Scripps	2100-2330	Last Quarter—New	20.5	90	Excellent
Aug. 7	6	Scripps	2130-2250	Last Quarter	21.5	70	Good
Sept. 12	4	Scripps	2210-2250	New	18.5	60	Fair
Sept. 22	0	Scripps	2030-2120	Full	18.0	20	Fair
Oct. 11	0	Scripps	2100-2230	New	18.0	50	Good
Oct. 20	0	Scripps	2000-2130	First Quarter	17.2	30	Fair

[1]The suitability of conditions for collecting pueruli was determined subjectively from general observations of current direction and velocity, wave height, and water clarity during the collecting period.

localities and work there was discontinued. Night-lighting observations during 1969 at the Scripps Institution pier provided a more complete picture of the apparent seasonal occurrence of pueruli, which first appeared in late May and were not observed after 4 September 1969.

These initial night-light studies allowed several interesting new observations on puerulus behavior. Previous investigators who reported that pueruli were occasionally attracted to night-lights (Harada 1957; Johnson 1960) presumed that the pueruli were lured off the bottom from rocky habitats where they had settled. However, this apparently was not the situation at the Scripps Institution pier for the following reasons.

The natural bottom substrate adjacent to the Scripps Institution pier for a radius of at least 500 m is entirely surf-washed sand. There is a small intertidal and subtidal rocky area approximately 500 m to the north, and an extensive rocky shoreline begins approximately 2 km to the south. While the pier pilings might afford a suitable habitat, we observed no pueruli or juveniles in several careful daytime and nighttime examination of the pilings, using scuba, during periods when there was active puerulus settlement in the habitat traps. In addition, direct observations of the free-swimming pueruli indicated that many individuals approached the light from a direction opposite that of the pilings. Perhaps most significant was the observation that the pueruli were seen swimming in only the top few centimeters of water; no individuals were ever seen approaching the light from a greater depth.

This opportunity to observe the free-swimming puerulus stage of *P. interruptus* thus demonstrated that, at least under these conditions, it is a surface-dwelling organism which occurs only in the top few centimeters of water. Consequently, the inconsistency or failure of standard plankton net tows to collect pueruli of this and other species probably is not due to the presumed benthic habits of this stage, but rather to improper sampling techniques. Only nets extending above the surface, and streamed parallel to the vessel's course with an unobstructed path, appear to be suitable. The likelihood of net avoidance accounting for previous failures seems minimal, as the pueruli of this species are relatively slow moving and easily captured in a hand held dip net, at least near a night-light.

Puerulus swimming speed in nature was measured by timing the passage of an individual between two lines suspended from a 2 m long, horizontally oriented pole, as it approached the underwater light. The mean swimming speed of six different pueruli under these conditions was 8 cm/s (range 6 to 9 cm/s). Individuals appeared to maintain this speed continuously, unless disturbed. In response to disturbance, they would spread their antennae and legs, sink slowly 5-20 cm, and then resume normal surface cruising with antennae held together and legs withdrawn. Illustrations of these swimming and sinking postures are shown in Figure 5.

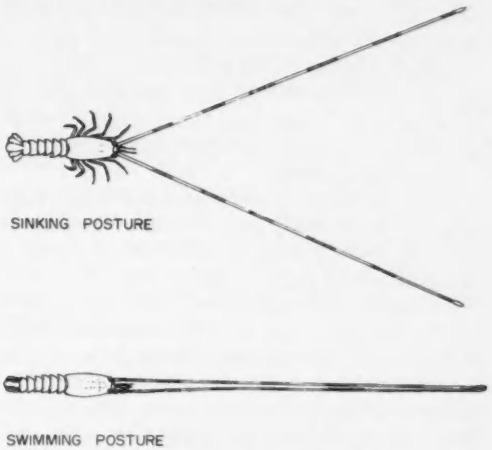

FIGURE 5.—Sinking and swimming postures of the puerulus larval stage of *Panulirus interruptus* as observed under a night-light.

Puerulus Pigmentation in Relation to Date of Settlement

Newly settled pueruli, or those collected during night-lighting, were always completely transparent. Pueruli held in open and closed system aquaria provided with *Phyllospadix* or other intertidal flora and fauna almost immediately began acquiring pigmentation, and this continued at a rapid rate. At temperatures of 18-20°C, pueruli would change from complete transparency to nearly complete pigmentation within 9-10 days, and would then moult into the first postpuerulus stage.

This occurred consistently among over 50 individuals we held in aquaria and observed systematically. Thus, the degree of pigmentation provided a reliable method of determining, within 1-2 days, the date of settlement. This technique

provided a more accurate means of evaluating possible correlations between puerulus recruitment and changing environmental factors than by merely recording the date on which the habitat trap was examined, as done by Witham et al. (1968) and Sweat (1968). In his later study, Parker (1972) provided a more detailed description of the pigmentation and transformation of the puerulus and postpuerulus stages of *P. interruptus*.

Laboratory observations indicated that once the puerulus settled in a suitable substrate, its transformation into a postpuerulus proceeded without delay. However, a few individuals which were held in containers without fresh *Phyllospadix*, algae, or rocks containing epifauna, remained as transparent pueruli for 2-3 wk until death, suggesting strongly that the presence of such suitable habitat features is necessary to induce transformation to the postpuerulus stage.

After settlement, pueruli became photonegative and were never again seen swimming. In order to test the related question of whether or not a settled puerulus might desert a habitat trap upon its removal from the water, and thus produce unreliable trap catch data, one seaweed frame habitat trap and one Witham trap containing known numbers of pueruli were returned to the water for 5-10 min on two different occasions, and then retrieved. No individuals left either the Witham or seaweed traps. This, and the laboratory observations described above, indicate that the number of individuals found in a habitat trap probably is a reliable estimate of the number that settled there.

Comparison of Habitat Trap Types

Habitat traps were mounted either singly or in groups of two or three from one main support bar in order that at least six different types could be tested simultaneously from the three available Scripps Institution pier positions (position A, B, or C, as shown in Figure 1). The exact pier position and combinations of traps were alternated from time to time, as indicated in Table 2, in order to compensate for possible variations in unknown factors influencing puerulus settlement, such as current direction, eddies near the pilings, and differences in daytime or nighttime light intensities. The results of comparative habitat trap design studies conducted during the summer of 1969 are summarized in Table 2. These results indicate that all habitat traps containing natural seaweed proved markedly superior to the Witham artificial habitat trap for this species (Figure 2C).

Only 5 pueruli were collected by two Witham habitat traps ($\bar{x}$ = 2.5 per trap), while 97 pueruli were collected by four seaweed habitats ($\bar{x}$ = 24.2

TABLE 2.—Results of a comparison of the catch effectiveness of habitat traps suspended off the Scripps Institution pier. The catches of pueruli per trap are also recorded in terms of the specific location of the trap at the pier (a, b, or c). Positions A and B were lighted, while position C was unlighted, as shown in Figure 1. For descriptions of the habitat trap designs, see Figure 2 and text.

Date traps examined 1969	Duration of sampling period (days)	Number of pueruli collected in habitat traps						
		Seaweed habitat traps				Witham habitat traps		Total collected
		Double frame	Single frame	Bag	Screen	#1	#2	
June 14	6	—[1]	2 a	—	—	0 a	—	2
20	6	—	—	—	—	—	—	—
27	7	—	—	—	—	0 a	—	0
July 2	4	0	7 a	—	—	1 a	—	8
5	3	3 b	1 a	—	—	0 a	—	4
9	4	3 b	1 a	—	—	0 a	—	4
13	4	2 b	1 a	—	—	0 a	—	3
17	4	3 b	0 a	—	—	0 a	—	3
23	6	3 b	1 a	—	—	1 b	—	5
28	5	1 b	1 a	—	—	0 b	—	2
Aug. 4	6	23 b	2 a	—	—	1 b	—	26
6	2	2 b	1 a	—	—	0 b	—	3
10	4	1 a	4 b	0 c	0 c	0 c	0 b	5
16	6	3 a	8 b	1 c	0 c	0 c	0 b	12
27	11	2 a	12 b	1 c	1 c	0 c	1 b	17
Sept. 4	8	1 a	1 b	0 c	0 c	0 c	1 b	3
12	8	0 c	0 c	2 b	1 b	0 c	0 b	3
19	7	0 c	1 c	1 b	0 b	0 c	0 b	2
27	8	0 c	0 c	0 b	0 b	0 c	0 b	0
Oct. 3	6	0 c	0 c	0 b	0 b	0 c	0 b	0
Total		47	43	5	2	3	2	102

[1]Habitat trap not in position at this time.

per trap), when all were in continuous use during the same 90-day time period from June through September 1969 (Table 2). Comparison of these catch figures by a chi-square test for equality indicates that the mean catch of the seaweed traps was significantly higher than that of the Witham traps ($P < 0.05$). The Witham habitat trap was not effective, either when new or moderately fouled with a variety of sessile organisms, yet the natural seaweed habitat traps appeared to catch well regardless of the condition of the plant material. Variations in the abundance of pueruli throughout the summer and differences in settlement in the different habitat positions, as discussed in subsequent sections, did not allow specific comparisons to be made between results of the habitat trap designs listed in Table 2. Yet general comparisons indicate that there were no major differences in catch between these trap designs that are not attributable to the environmental causes discussed in subsequent sections below. However, the nylon bag habitat trap (Figure 2E) proved to be the best in terms of cost, ease of use, and durability. It also appeared to catch as well as the other types, although tests were begun too late in the final puerulus settlement season during which we sampled to verify this. Thus, the bag trap design is recommended for future studies of this nature, and was used by Parker (1972) in a later study.

Habitat Trap Success in Relation to Position on the Pier

A comparison of the catch results of the "double" and "single" frame seaweed habitat traps, as shown in Table 2, indicates that more pueruli were consistently collected from the B than the A position on the Scripps Institution pier (Figure 1), when either type of trap was placed there. A combined total of 65 larvae was collected in the B position, versus only 24 in the A position by these two traps during the same 82-day period from 2 July to 19 September. A comparison of these catch figures by a chi-square test for equality indicates that the catch at position B was significantly greater than at position A ($P < 0.05$). No explanation for this difference is apparent at the present time, but it seems to indicate that there may be subtle environmental effects which influence puerulus settlement in habitat traps to a greater extent than do variations in trap design.

Significance of Nocturnal Illumination of Traps in the Attraction of Pueruli

The strongly positive phototactic response exhibited by the puerulus stage during night-lighting observations suggested that nocturnal illumination may play an important role in the successful operation of habitat traps. To evaluate this, additional traps were maintained in an unlighted area of the Scripps Institution pier (area C in Figure 1).

The results, summarized in Table 3, indicate that during the period from 10 August to 29 September 1969, when each trap design was maintained at both the lighted (positions A and B) and nonlighted (position C) pier locations, all traps caught more larvae in the lighted positions. A total of 38 larvae were collected over 132 "trap-days" (1 trap in place for a 24-h period = 1 trap-day) in the lighted position, versus only 4 per 132 trap-days in the nonlighted position. Comparison of these total catch values by means of a chi-square test for equality indicates that the value for the lighted positions was significantly greater than for the unlighted one ($P < 0.05$). This suggests that noc-

TABLE 3.—A comparison of the number of pueruli caught in lighted and nonlighted habitat traps. For detailed descriptions of trap types, and lighted and nonlighted pier positions, see text and Figures 1 and 2.

Type of habitat trap	Lighted (positions A and B)			Nonlighted (position C)		
	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days	No. individuals collected per trap	Sampling period (days)[1]	Catch per 20 trap-days
Double frame	7	29	4.8	0	15	0
Single frame	25	29	17.2	1	15	1.32
Bag	3	15	4.0	2	29	1.38
Screen	1	15	1.32	1	29	0.68
Witham "a"	—[2]	—	—	0	44	0
Witham "b"	2	44	0.48	—	—	—
Mean catch per 20 trap-days			5.4			0.68

[1]Number of trap days during the period of 10 August to 29 September only (see Table 1).
[2]Habitat trap not in place.

turnal illumination plays a major role in the successful use of these habitat traps for pueruli of *P. interruptus*. The fact that no pueruli were caught in the unlighted habitat traps maintained offshore, as discussed in the next section, provides additional strong support for this conclusion.

Habitat Traps Maintained Offshore

Unlighted habitat traps of the "bag" and "screen" designs were anchored in water 3- to 15-m deep in the San Diego area off Point Loma, La Jolla, and off the northeast shore of Catalina Island, Calif., at the positions shown in Figure 6a, b. This was done to monitor the recruitment of pueruli at other locations along the San Diego coastline, and on the leeward side of a large offshore island, as well as to determine the importance of lights in attracting pueruli by comparing these unlighted traps with those placed under the Scripps Institution pier lights. The traps placed offshore were checked and refilled with fresh *Phyllospadix* and red algae every 10-15 days during August and September 1969. Many were lost, apparently because of entanglement with kelp and boat propellers. However, the large number maintained successfully failed to collect any pueruli, despite the fact that puerulus settlement at the Scripps Institution pier was relatively high during this same period. The four traps maintained at Catalina Island were situated directly above a shallow rocky area, approximately 2-6 m in depth, where we had observed many small first year juvenile lobsters the previous winter. We presumed that the presence of these young juveniles indicated that this was an area of high puerulus recruitment. Thus, failure of the unlighted traps to collect pueruli at this location was particularly surprising.

The failure of these offshore habitat traps may have been due not only to the lack of nocturnal illumination, but also to the presence of large quantities of *Phyllospadix* and algal flotsam in the areas where they were maintained. The probability of a puerulus settling in a seaweed habitat trap under such conditions would be small, considering the large volume of seemingly equally suitable patches of floating surfgrass and algae present in these areas. In contrast, relatively few masses of plant flotsam of this kind were observed in the area around the Scripps Institution pier.

In an attempt to evaluate this, many clumps of floating *Phyllospadix* were collected and examined for pueruli while deploying and checking the offshore habitat traps. No pueruli were found in this manner, but only a relatively small percentage of this material was examined relative to that present, thus leaving the question open to further investigation.

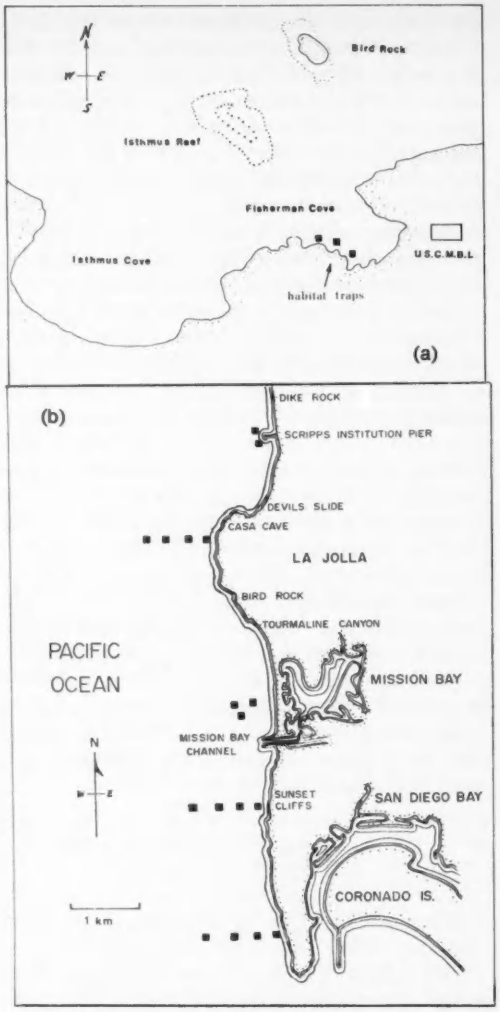

FIGURE 6.—Locations of sampling areas off northeastern Catalina Island (a) and San Diego (b) for puerulus and early juvenile *Panulirus interruptus*.

Neuston Net Sampling

Semiquantitative sampling with the paired

neuston nets was initiated late in the study, during the period 3 September to 12 October 1969 (Table 4). The results of the habitat trap collections (Table 2) suggest that these towing operations were conducted during a period of very low puerulus abundance, yet two pueruli were collected during two separate towing efforts. Unfortunately, it was not possible to complete the development of these nets and begin sampling operations during the summer period of peak puerulus abundance.

Concurrent studies of the distribution and abundance of the phyllosoma larval stage of *P. interruptus* in the same inshore areas, using standard 1 m and larger conical nets in surface and oblique towing patterns, failed to catch any pueruli (W. E. Hazen and J. H. Rutherford, pers. commun.). In addition, considering that Johnson (1956, 1960) obtained only a few pueruli during 7 yr of extensive sampling with surface and oblique hauls of a 1-m conical net, our preliminary results suggest that use of this neuston net system probably is a more effective sampling technique and should be thoroughly evaluated in future studies. These results also strengthen the argument that the puerulus is pelagic, occurs at the surface, and is a temporary member of the neuston community.

Relationship of Puerulus Settlement to Environmental Factors

Efforts to relate the influx of pueruli in major environmental factors, such as temperature, salinity, and lunar phase, were complicated by lack of information concerning other unmeasured or unknown variables which may have subtle effects on the settlement of pueruli in the habitat traps. These may include specific wave characteristics, current velocity and direction, and water turbidity. Therefore, the apparent low abundance of pueruli during some periods might be due to their failure to settle in the habitat traps, rather than their absence from coastal waters. Variations in surface salinity levels of water masses along the open coast when our sampling was conducted were very slight. Consequently, the influence of this factor probably was negligible and showed no obvious relationship to puerulus settlement, based on data available for the area of the Scripps Institution pier. Variations in wave heights and surf conditions occurring at the Scripps Institution pier during the summer also were relatively small.

TABLE 4.—Results of puerulus sampling with paired neuston nets.

Date 1969	Time	Surface area sampled (m^2)[1]	Water volume sampled (m^3)[1]	San Diego sampling localities	Number collected
3 Sept.	1400-1500	800	400	Mission Bay	0
10 Sept.	2000-2100	800	400	Mission Bay Channel	0
10 Sept.	2130-2230	800	400	Mission Bay Channel	1
20 Sept.	1800-1840	500	250	Off Pacific Beach	0
20 Sept.	1900-1930	300	150	Off Pacific Beach	1
7 Oct.	2000-2100	800	400	Off Pacific Beach	0
12 Oct.	1200-1330	1,000	500	Mission Bay Channel	0

[1]Estimated from average boat speed and duration of tow.

The range in height of swells recorded at the pier was 0.3-0.9 m (1-3 feet), and showed no obvious pattern in relation to puerulus settlement. However, the following general relationships between puerulus settlement and environmental conditions seem apparent.

Seasonal Periodicity

The results of night-lighting during 1969 (Table 1), and habitat trap sampling conducted in 1969 (Table 2) are presented together in Figure 7. These data indicate that the pueruli of *P. interruptus* began to appear in nearshore San Diego waters during late May, and occurred there continuously until mid-September, apparently reaching their greatest abundance during the first week of August. The habitat traps could not be maintained during rough winter surf conditions, and occasional night-light efforts during the winter were unsuccessful, so we were not able to establish conclusively that pueruli are absent from nearshore waters between October and May. However, evidence presented by Johnson (1960) on the seasonal periodicity of the later phyllosoma stages of *P. interruptus*, which are abundant only during the period from January to June, suggests that there would be no major influx of pueruli during the winter months, although a small number of individuals might be present throughout the year.

Relationship to Water Temperature

A comparison between surface water temperatures and puerulus trap catches obtained at the Scripps Institution pier indicates that the

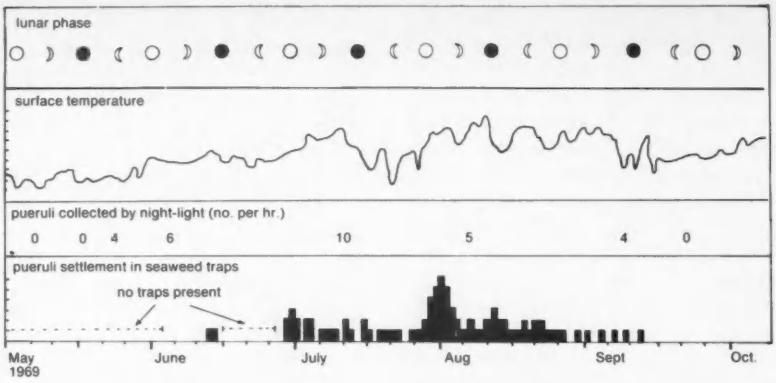

FIGURE 7.—Relationship of puerulus settlement to lunar, temperature, and seasonal cycles. The habitat trap catches are presented as catch per unit effort, and represent the total combined catch of two seaweed traps (primarily the single and double frame designs, Figure 2) maintained in the lighted pier positions (a and b). The date of original settlement for each puerulus was estimated within 1 to 2 days by its degree of pigmentation. Temperature data are from Scripps Institution pier records.

prevailing influx of pueruli corresponds with the seasonal period of highest temperatures, as shown in Figure 7. The peaks of puerulus settlement occurring during the first weeks of July and August also appear to correspond with periods of rising water temperatures. However, another possible interpretation of the settlement patterns shown in Figure 7 is that the low abundance of pueruli observed during the period of 10-25 July may have been caused by an influx of cold water originating from local submarine canyon upwelling, which occurs periodically. Such a cold upwelling water mass would not be expected to contain any pueruli if the surface-swimming habits attributed to this stage are correct, and could effectively prevent pueruli in warmer water masses from entering the pier area we sampled.

Lunar Perdicity

Studies by Witham et al. (1968) and Sweat (1968) of *P. argus* pueruli in Florida and by Phillips (1972) of *P. longipes cygnus* pueruli in Australia determined that puerulus settlement was highest during the new moon phase and did not occur at all during full moon periods. The abundance of *P. interruptus* pueruli, on the other hand, did not show any evident relationship to lunar phases. On two occasions during the first parts of July and August, there were apparent peaks in puerulus abundance during the full moon phase, as shown by the habitat trap results in Figure 7. Night-light and habitat trap collections and their relationship to lunar phases are summarized in Table 5. These data indicate that there were no lunar periods when pueruli of *P. interruptus* were not present and did not settle, and thus that they apparently do not respond to lunar cues, or at least not in the same manner as do species studied elsewhere.

Witham et al. (1968), Sweat (1968), and Phillips (1972) were unable to determine whether the absence of pueruli from their habitat traps during full moon periods was due to their absence from the area or their avoidance of the traps. The fact that pueruli of *P. interruptus* were present and settled in our habitat traps directly under the bright lights of the Scripps Institution pier in-

TABLE 5.—The relationship between lunar phases and puerulus abundance, as determined by habitat trap and night-light results. Total catches, given in detailed form in Tables 1 and 2, are presented below as catch per unit effort.

Lunar phase (eight equal divisions)		Habitat trap (mean catch/hour)[1]	Night-light (mean catch/hour)[2]
Full moon	(1)	5.0	3.0
	(2)	2.5	4.0
Last quarter	(3)	1.7	4.0
	(4)	1.7	10.0
New moon	(5)	2.0	1.0
	(6)	1.5	3.0
First quarter	(7)	1.8	6.5
	(8)	1.0	0.0

[1]Based on catches of the single and double frame traps only.
[2]Periods of poor conditions (i.e., unsuitable for observing pueruli) were excluded from calculation of the mean.

dicates that, at least for this species, illumination is not an inhibitory factor. In fact, it may serve as a stimulus for settlement.

In this regard it is important to note that persistent stratus overcast in the southern California coastal zone during the summer months results from upwelled water coursing southward from Point Conception. Thus, normal background illumination from the moon and stars generally is eliminated, although sky glow is present near major coastal cities. Consequently, at our sampling site the prevailing overcast and nocturnal illumination from the Scripps Institution pier lights could have masked any lunar effect, resulting in what we observed, puerulus settlement in traps during all moon phases.

Duration of the Puerulus Stage

Essentially nothing is known about the duration of the puerulus stage of any spiny lobster species. Sheard (1949) suggested that the puerulus of the western Australian spiny lobster, *P. longipes cygnus*, lasts for 2-3 wk, but offered no supporting evidence.

April was consistently the period of greatest abundance for the last phyllosoma stage (stage 11)

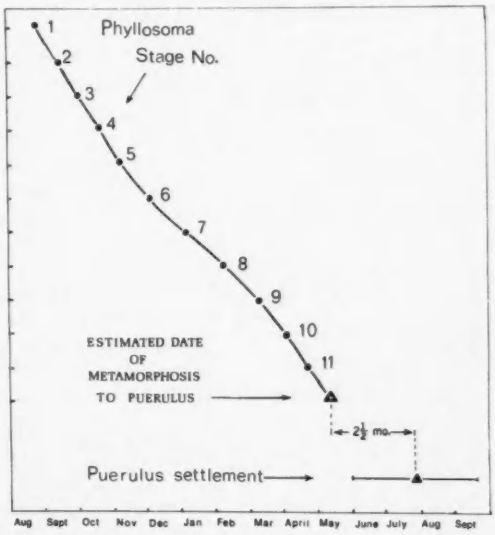

FIGURE 8.–Comparison of seasonal occurrence and dates of greatest abundance of the phyllosoma and puerulus larval stages. Data on the phyllosoma stages are from Johnson (1960).

of *P. interruptus*, based on evidence obtained by Johnson (1960) in extensive sampling during the period 1949-1957, as summarized in Figures 8 and 9. Most of the late stage phyllosoma larvae he

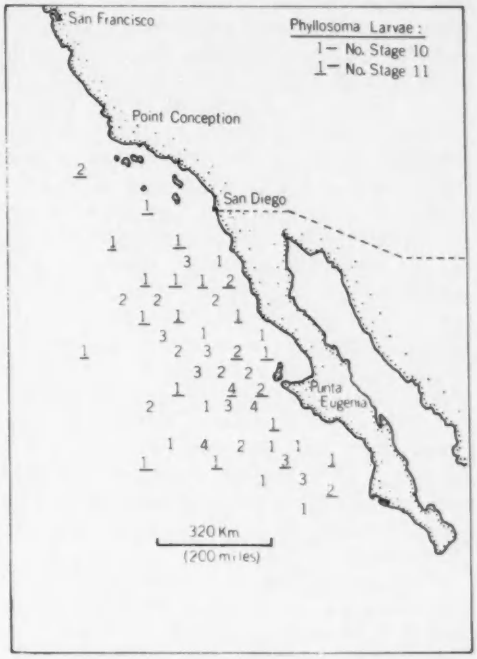

FIGURE 9.–Offshore distribution of the late stage phyllosoma larvae (stages 10 and 11) of *Panulirus interruptus* during the period from 1949 to 1955, as reported by Johnson (1960).

collected were taken at stations 160-320 km (100-200 miles) offshore (Figure 9). Our data indicate that the greatest abundance of pueruli in coastal waters during 1969 was in early August, approximately 3½ mo after this peak in the abundance of stage 11 phyllosomes. Assuming that the duration of the eleventh phyllosoma stage extends for a period of 1 mo, and that shoreward migration is accomplished by the puerulus, rather than by the last phyllosoma larval stage (see subsequent discussion), then this suggests that the puerulus stage of *P. interruptus* may have an average duration of approximately 2½ mo. This timing is represented diagrammatically in Figure 8. Thus, a period of 2-3 mo appears to be a reasonable estimate for the average duration of the puerulus stage.

DISCUSSION

Mode of Life of the Puerulus Stage

Johnson (1960) and Lindberg (1955) speculated that the puerulus of *P. interruptus* is a benthic form, largely because it occurs so infrequently in standard net tows. However, the results of this study strongly suggest that it is a pelagic form, and in particular a member of the surface-dwelling neuston. Several lines of evidence support this conclusion. Our observations of many free-swimming pueruli which were attracted to night-lights revealed that the pueruli always swam in the top few centimeters of surface water, and no individuals were ever observed moving toward the light from deeper water. Pueruli were readily collected in habitat traps floating at the surface. However, the occurrence of pueruli at greater depths cannot be ruled out on the basis of habitat trap evidence alone because the traps were not maintained at greater depths. Although preliminary and very limited, our surface sampling with neuston nets yielded a much higher catch per unit effort than did standard near-surface and oblique tow sampling methods employed by previous investigators.

The puerulus stage of *P. interruptus* also has specialized physical characteristics which suggest that it is adapted to a pelagic existence. These include: 1) heavily setose pleopods and a streamlined body for efficient, forward swimming; 2) a transparent body completely devoid of pigmentation; and 3) extremely long, delicate antennae which appear unsuitable for a benthic existence because they quickly break off upon settlement. In addition, at the time the puerulus moults into the first postpuerulus stage, it loses the setose pleopods and acquires stronger antennae, an expanded cephalothorax, and walking ability typical of later demersal stages. In fact, pueruli we collected and held in aquaria were never observed walking upon the substrate, instead only clinging to algae or crevices in rocks and shells. A more detailed description of this transformation process from puerulus to postpuerulus was developed in a subsequent study by Parker (1972).

Both Witham et al. (1968) and Phillips (1972) reported that, in comparative tests between habitat traps maintained on the surface and traps anchored 1-4 m below the surface, all but a few pueruli of *P. argus* and *P. longipes cygnus* were collected in those at the surface. Phillips collected only 1 out of 38 pueruli in traps at 4-m depth, and Witham collected 12 from one trap anchored on the bottom in water 1 m deep, as compared to an average of 27 pueruli in surface traps located nearby.

Sweat (1968) utilized a multiple plankton net array for studying the depth preference of *P. argus* pueruli in the Florida Keys area. This system consisted of three conical plankton nets mounted from a bridge across a shallow channel connecting Florida Bay with the Atlantic Ocean. The nets were suspended at the surface, at mid-depth (1 m), and on the bottom (2.3 m), and were operated for 2-h periods within the new moon phase during evening flood tides. The largest proportion of the pueruli were collected by the mid-depth net (116 at the surface, 418 at 1 m, 61 at 2.3 m depth). However, this may have been due to the particular conditions in the channel, including its shallow depth, water turbulence, and the possibility that the pueruli were in the process of settlement at the time of sampling.

In general, these observations by Sweat (1968), Witham et al. (1968), and Phillips (1972) agree with ours on *P. interruptus*. The pueruli of these species seem to be restricted primarily to the ocean surface, at least just prior to settlement.

The Functional Significance of the Puerulus Stage

On the basis of morphology and our observations of its behavior, the puerulus stage of *P. interruptus* appears to be well adapted for directed, forward swimming, as shown in Figure 5, rather than for the passive, pelagic existence apparently exhibited by all phyllosoma larval stages of spiny lobsters. What, then, is the purpose of this directed swimming? A possible answer is suggested by considering the early life history of the scyllarid lobster, *Scyllarus americanus*, which also has a phyllosoma larval stage but no transitional puerulus stage, moulting instead directly into a nonswimming, benthic juvenile (Robertson 1968). Some other scyllarid species have a transitional form called a puerulus or, more properly, a nesto stage. The phyllosoma larval period of *S. americanus* is quite short (4-5 wk), thereby allowing the larvae a much greater chance of remaining near the shallow coastal areas suitable for later demersal life. In contrast, the phyllosomes of palinurid lobsters and other species of scyllarids may be carried several hundred kilometers out to

sea during their typical 5-10 mo larval existence. Obviously, the larvae must return not only to the coastal area, but also to very shallow nearshore zones if they are to transform and become established as demersal juveniles.

Previous investigators (Lindberg 1955; Johnson 1956, 1960, 1971; Saisho 1966; Sims and Ingle 1966; Lazarus 1967; Chittleborough and Thomas 1969; Chittleborough 1970) have postulated for several species that this recruitment in nearshore waters takes place during the phyllosoma stage, possibly through the action of countercurrents, upwelling, and eddies. Several studies, particularly those of Johnson (1960) and Chittleborough (1970), have shown clearly that large numbers of late stage phyllosoma larvae do remain well within the coastal areas in which the earlier larval stages occur. Evidence presented by Johnson (1960) also has shown that hydrography plays a major role in retaining a supply of late stage phyllosomes, and presumably pueruli, within reasonable distances from the coast. The presence, within one net haul, of several different phyllosome stages that must have been produced months apart, and the presence of late stage phyllosomes at the same locality, is good evidence that mixing processes and retaining eddies prevent wholesale flushing of these larvae from the coastal area. However, the late stage phyllosomes seem to be concentrated primarily in areas 50-250 km offshore, and the specific mechanism of onshore movement and recruitment has not been demonstrated.

If there were major active or passive movements of late stage phyllosomes toward shore, then one would expect to find relatively large numbers of them in shallow, inshore waters as well, or at least a trend in this direction. Most of the sampling reported by Johnson (1956, 1960) was conducted in waters 8 or more kilometers ($\geq$ 5 miles) offshore. However, studies of the distribution and abundance of phyllosoma larvae of *P. interruptus* in San Diego waters much closer inshore by W. E. Hazen and J. H. Rutherford (pers. commun.) during the summer months of 1969-1970, employing surface and oblique net tows, failed to collect any individuals older than stage 2. This suggests that the later stages occur either many kilometers offshore, as observed by Johnson (1956, 1960), or are concentrated in unknown areas.

For lack of evidence to the contrary, it has also been suggested that these phyllosoma larvae occurring far offshore are lost to the population and must perish. For similar reasons, Lindberg (1955) and Johnson (1960) have speculated that when these phyllosomes moult into the puerulus stage, the puerulus quickly settles to the bottom while still in deep water. Presumably, some of these are then able to migrate onshore to the shallow coastal nursery areas as benthic puerulus or postpuerulus forms.

However, in light of our behavioral observations on both pueruli and juveniles, another more likely explanation is that the puerulus stage may have evolved specifically for this purpose of recruitment. These observations suggest to us that the puerulus is a transitional, pelagic stage specifically adapted for directional swimming, and that it is capable of returning by active means to nearshore nursery areas suitable for settlement, thereby fulfilling the key role in recruitment. During this process, the surface-swimming and associated positive phototactic behavior of the puerulus stage probably aid it in locating the shallow nearshore areas which our related observations suggest are required as nursery grounds for the early juvenile stages.

Exactly how important a role the puerulus stage plays in the recruitment of the demersal population probably depends on three factors: 1) the degree of "assistance" contributed previously by the late phyllosoma stages which may move actively, e.g., by vertical migrations, into shoreward-directed currents or eddies; 2) how effective the puerulus is in travelling over long distances, with regard to both swimming speed and endurance; and 3) how well the puerulus can navigate, considering the fact that aimless wandering or swimming away from the coast would markedly reduce its probability of survival.

It seems reasonable to expect that the puerulus can swim nearly continuously, as other nektonic crustaceans, such as euphausiids, apparently do. If so, our estimate of an 8 cm/sec average swimming speed for the puerulus indicates it has the potential to travel approximately 7 km (4.3 miles) per day, or about 500 km (350 miles) during the period of 80 days estimated as the approximate average duration of this stage. Thus, the 160-320 km (100-200 mile) distance from shore at which Johnson (1960) found most late stage *P. interruptus* phyllosomes (Figure 9) could be within the basic swimming capabilities of the puerulus stage, even if part of the time was spent swimming against surface currents or in an inactive state.

The current patterns off the southern California and Baja California coasts are complex, and have

been studied extensively (see, for example, Johnson 1956, 1960; Wyllie 1966). During the summer months the California Current system has a generally southward trend, but displays retaining eddies and a net northward onshore drift in the northern range of *P. interruptus* larval distribution near the southern California coast and adjacent Channel Islands. There is a net southerly or offshore drift for water masses off most of Baja California. Even the apparent swimming capabilities of the puerulus stage probably would not allow it to move against these strong, offshore surface currents, particularly because an object in the surface waters would be vectored at a 45° angle, or westwardly, to the wind and current forces.

As a specific example of this problem, review of mean geostrophic flow at the surface off California and Baja California for the months of June-September during the typical period 1950-1964 (Wyllie 1966) reveals that there was a net surface transport southward from Point Conception to Cabo San Lucas offshore from approximately 80-320 km (50-200 miles). Northward flow near shore during these summer periods occurred only in the Southern California Bight (San Diego to Ventura), while net offshore transport apparently occurred from Bahia San Quintin south to Cabo San Lucas as a precursor to the California Current Extension.

Thus, it appears very likely that a majority of the late stage phyllosoma and puerulus larvae in the surface layers in this region, more than about 40-95 km (25-60 miles) offshore, depending on variations in the current system, were swept seaward by geostrophic flows which averaged greater than 46 cm/sec (0.9 knots) during this typical 15-yr interval. Such individuals undoubtedly are lost to the population. On the other hand, individuals present closer to shore, or in retaining eddies near the Southern California Channel Islands and the shallow Bahia Sebastián Vizcaino-Isla Cedros area (Johnson 1960), are within distances and ocean surface conditions which would allow their nearshore recruitment by directed swimming of the puerulus stage.

The Significance of *Phyllospadix* in the Settlement of the Puerulus Stage

The strong preference by the puerulus stage for the habitat traps containing *Phyllospadix torreyi*, as compared to generally similar synthetic material in the Witham traps, seems particularly significant in view of the fact that both Serfling (1972) and Parker (1972) discovered numerous early juvenile stages primarily in areas which had thick growths of this surfgrass. Comparative evaluations of habitat traps filled with *Phyllospadix* and other substrates, such as giant kelp (*Macrocystis pyrifera*) fronds and holdfasts, the eelgrass (*Zostera marina*), and *Mytilus* clumps, might prove useful as a means of improving collection success with the traps.

Preference tests involving various substrates typical of different nearshore habitats might also suggest other areas of natural puerulus settlement. In this regard, however, substrate preference tests of the puerulus and postpuerulus stages conducted in the laboratory by Parker (1972) suggest that these stages favor *Phyllospadix* over *Macrocystis*, *Zostera*, several species of red algae, sand, and rock.

Evaluation of the Natural Seaweed and Artificial Habitat Traps

In comparative tests conducted by Witham et al. (1968), their Witham habitat trap proved somewhat more successful than two other seemingly poor refuges, a tire and a shingle (102 versus 77 and 57 pueruli collected, respectively, over a 10-mo period). Phillips (1972), studying *P. longipes cygnus* in Australia, found that his artificial seaweed habitat trap design collected more pueruli than a modified Witham trap, but only by a factor of approximately two. In contrast, the results of our comparative evaluations (Table 2) indicate that the average number of pueruli caught by the two lighted natural seaweed habitat traps (single and double seaweed frame) was 47 per trap, while on lighted Witham artificial substrate trap caught only 5 pueruli over the same time period and at the same location. This suggests that the natural seaweed trap design was approximately nine times more effective than the Witham trap. Secondly, the lighted habitat traps, regardless of the design, caught more pueruli than did nonlighted ones at the Scripps Institution pier during the same time period (33 and 7 pueruli respectively), suggested that a lighted trap was approximately four to five times more effective than an unlighted one. Thus, the system developed in this study, utilizing a combination of both nocturnal illumination and natural seaweed, clearly is much more effective in collecting pueruli of *P. in-*

terruptus than the nonlighted artificial habitat system utilized by Witham et al. (1968).

This suggests that natural seaweed habitat traps filled with native flora characteristic of juvenile habitats, in combination with nocturnal illumination, could prove to be a more successful means of sampling the pueruli of other spiny lobster species as well. If so, use of this modified sampling technique might indicate that the abundances of *P. argus* pueruli in Florida and those of *P. longipes cygnus* in Australia actually are much greater than previously estimated by Witham et al. (1968), Sweat (1968), and Phillips (1972).

Implications for Aquaculture and Fishery Management

If the small numbers of pueruli captured during this study are representative of puerulus availability throughout the geographic range of *P. interruptus*, large-scale collecting of this stage for purposes of aquaculture and restocking is not feasible and probably could not be justified. However, other locations, particularly those closer to the center of adult and larval concentrations, such as the Bahia Sebastián Vizcaino-Isla Cedros area off Baja California (Figure 9), should be investigated as potential sites for such large-scale collecting operations, as well as for purposes of locating the primary areas of puerulus settlement.

It also seems reasonable that the habitat trap collecting system developed in this study, if standardized and employed on a wider geographic scale, could prove useful for monitoring fluctuations in year class recruitment of pueruli, and thereby provide a means of predicting fluctuations in the size of the demersal population in following years. For example, an extension of our study by Parker (1972) during the years 1970-71 indicates that puerulus settlement at the Scripps Institution pier was much less than we observed during the same months in 1969. If this reduced recruitment was representative of a wider geographic area, then the size of the adult population available to the commercial fishery within the succeeding 5-8 yr might be expected to show corresponding changes.

SUMMARY

Basic ecological and behavioral information was obtained about the recruitment process, habitat preferences, and general abundance of the puerulus larval stage of *Panulirus interruptus*.

Pueruli of *P. interruptus* exhibit a strong positive phototactic response, and could be lured to a bright underwater night-light from the surface water surrounding the Scripps Institution of Oceanography pier.

Direct observations of free swimming pueruli by this method demonstrated that this stage is typically pelagic rather than benthic, and swims at the surface in a continuous and directed manner. Estimates of swimming speed were obtained.

The surface swimming behavior of this stage indicates that it probably can be properly sampled quantitatively only by large nets towed horizontally at the surface. This may explain why few pueruli have been taken by other conventional sampling methods. Paired neuston nets were developed specifically for this purpose and pueruli seemed to be sampled effectively in this manner during preliminary evaluations.

Puerulus larvae also were collected effectively in floating habitat traps containing the surfgrass, *Phyllospadix torreyi*. A variety of natural seaweed habitat trap designs were tested, and all appeared to be about equally effective in collecting pueruli; however, a nylon bag habitat trap proved best in terms of cost and durability. All natural seaweed habitat traps were markedly superior in collecting pueruli compared to the Witham habitat trap design, formed of synthetic fibrous material.

Habitat traps maintained under the lighted end of Scripps Institution pier collected many more pueruli than those not subject to such artificial illumination. The failure of habitat traps placed offshore to collect any pueruli may have been due to the availability of abundant seaweed flotsam in the areas where they were maintained, as well as lack of artificial illumination. Both the presence of intertidal plants (particularly *Phyllospadix*) and nocturnal illumination appear to play significant roles in the settlement of puerulus larvae in habitat traps.

The results of night-lighting and habitat trap sampling indicate that off San Diego, Calif., the seasonal influx and settlement of puerulus larvae is continuous, beginning in May and ending in September.

Estimates based on a comparison of the peak periods of abundance for pueruli and the preceding final phyllosoma larval stage suggest that the puerulus stage of *P. interruptus* has a duration of approximately 2½ mo. This is followed by

settlement in shallow water and transformation to a benthic, postpuerulus form.

Based on observations of its surface swimming behavior and capabilities, preference for plant covered substrates, settlement behavior, and morphology, the puerulus appears to be a transitional, pelagic stage specifically adapted for directional swimming, whose function is to return from offshore by active means to nearshore areas suitable for settlement. Thus, it probably occupies the key role in recruitment.

The seemingly low abundance of pueruli in the southern California areas sampled suggests that it would not be practical or beneficial to attempt large collections there for purposes of aquaculture and restocking. However, other locations, including those closer to the center of the geographical range, should be investigated as potential large scale collecting sites.

Employed in a standardized manner, the habitat trap system developed in this study could prove useful in locating primary areas of puerulus settlement and in monitoring fluctuations in year class recruitment.

ACKNOWLEDGMENTS

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A THEORETICAL TREATMENT OF UNSTRUCTURED FOOD WEBS

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ABSTRACT

In a recent paper, Isaacs has proposed a model for an unstructured food web in which the interconnections are so diverse that all heterotrophs in the system can be treated as if they were at the same average trophic position. This paper recasts the original model in terms of a 3 × 3 matrix using three empirical constants. In this form, the model can be easily generalized to one having nine constants and reflecting a more realistic view of the interactions among levels of a community.

Recent papers by Isaacs (1972, 1973) proposed an alternative to trophic level schemes for representing interactions among species. He termed this an unstructured food web and proposed a "matrix"[2] technique (Isaacs 1972) for evaluating the equilibrium distribution of energy (or matter) which would result from these interactions. In this paper we propose an alternative formulation of Isaacs' model which utilizes classical matrix and operator techniques.

SERIES APPROACH

Isaacs' model was originally proposed to account for Young's data (Young 1970) from the Gulf of California which indicated that cesium was not found concentrated in ratios one would expect from a simple food chain. Isaacs assumes that the principal interconnections in the marine food web are so diverse that all heterotrophs in the system (from microorganisms to vertebrates) can be treated as if they derived their food from a common source that is only coarsely differentiated. Therefore, the heterotrophs can all be treated as if they were at the same average trophic position. In this unstructured food web, Isaacs visualizes four levels of matter or energy: 1) source, 2) living tissue, 3) nonliving but retrievable matter, and 4) irretrievable matter. The source is assumed to be phytoplankton which is added to the system at a constant rate. The living matter consists of all heterotrophs, while the dead retrievable matter may consist of such sources of carbon as organic detritus or dissolved organic matter. The irretrievable component is that matter (or energy) which is forever lost to the system through such processes as respiratory combustion or mineralization. The "unstructured" nature of the food web comes from a set of coefficients which represent movement of material between these groups. The transitions are not in a trophic level line. Rather, groups two and three interact bilaterally and groups three and four can receive from other levels bypassing intermediates.

Isaacs calculates the final steady state values for the total living and dead material by summing two infinite series. To obtain these series, he introduces a "matrix" which is designed to aid in the formulation of each of the terms. The series take the form:

$$\begin{aligned} M'_t = {} & M_0K_1 + M_0K_1(K_1 + K_3) \\ & + M_0K_1[K_1(K_1 + K_3) + K_3(K_1 + K_3)] \\ & + M_0K_1[K_1(K_1 + K_3)^2 + K_3(K_1 + K_3)^2] \\ & + \ldots = \frac{M_0K_1}{1 - (K_1 + K_3)} = \frac{M_0K_1}{K_2} \end{aligned}$$

$$\begin{aligned} M''_t = {} & M_0K_3 + M_0K_3(K_1 + K_3) \\ & + M_0K_3[K_1(K_1 + K_3) + K_3(K_1 + K_3)] \\ & + M_0K_3[K_1(K_1 + K_3)^2 + K_3(K_1 + K_3)^2] \\ & + \ldots = \frac{M_0K_3}{1 - (K_1 + K_3)} = \frac{M_0K_3}{K_2} \end{aligned}$$

where M_0 = increment of initial input periodically introduced into the

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[2]We have enclosed Isaacs' use of the word "matrix" in quotes because he has used the word in a common rather than in the standard mathematical sense. When the word appears without quotes in this text we are using it in the standard sense of a rectangular array of elements which operates on column vectors from the left to produce new column vectors.

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system at intervals equal to the time taken by one average step in the food web,

M'_t = total quantity of material in living tissue (level two),

M''_t = total in nonliving recoverable material (level three),

K_1 = a coefficient of conversion of matter (or energy) in food into living tissue,

K_2 = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization), and

K_3 = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter).

Restrictions on coefficients are:

$$K_1 + K_2 + K_3 = 1,$$
$$0 < K_i < 1, \text{ where } i = 1, 2, \text{ or } 3.$$

MATRIX APPROACH

In our representation of the unstructured food web, source, living tissue, and nonliving but retrievable matter are taken to be components in a vector in a three-dimensional space. This vector can be written

$$\overline{w} = \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix}$$

where w_1 is the amount of matter (or energy) present in phytoplankton, w_2 is the amount present in heterotrophs, and w_3 is the amount present in retrievable dead material. The fourth level (loss) is the difference between the total input and the material present in the three other levels.

The matrix operator controlling movement of material from one level to another, using Isaacs' coefficients, takes the form:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ K_1 & K_1 & K_1 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

Each K represents the proportion of material transferred between the levels appropriate to its position in a time equivalent to one application of the matrix.

As Isaacs points out, three constants may not be sufficient. It is probably not reasonable to assume, for example, that all matter is converted to living tissue with the same coefficient of conversion or that both living and dead matter have the same conversion factor to irretrievable form. One advantage of our method is that it can be generalized to a more complex form. This cannot easily be done with Isaacs' original method because crossterms in the K's rule out viewing the steady state values as simple geometric series. The generalized form of the matrix for an unstructured food web with these additional coefficients is:

$$A = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix}$$

where k_1 = conversion factor from source to living,

k_2 = conversion factor from source to dead retrievable,

k_3 = conversion factor from source to inrretrievable,

k_4 = conversion factor from living to living,

k_5 = conversion factor from living to dead retrievable,

k_6 = conversion factor from living to irretrievable,

k_7 = conversion factor from dead to living,

k_8 = conversion factor from dead to dead retrievable, and

k_9 = conversion factor from dead to irretrievable.

In this case,

$$k_1 + k_2 + k_3 = 1$$
$$k_4 + k_5 + k_6 = 1$$
$$k_7 + k_8 + k_9 = 1$$
$$0 < k_i < 1, \text{ where } i = 1 \text{ to } 9.$$

When this matrix acts upon the state vector $\overline{w}$ the result is somewhat more complex:

$$A\overline{w} = \begin{pmatrix} 1 & 0 & 0 \\ k_1 & k_4 & k_7 \\ k_2 & k_5 & k_8 \end{pmatrix} \begin{pmatrix} w_1 \\ w_2 \\ w_3 \end{pmatrix} = \begin{pmatrix} w_1 \\ k_1 w_1 + k_4 w_2 + k_7 w_3 \\ k_2 w_1 + k_5 w_2 + k_8 w_3 \end{pmatrix}.$$

Steady State Results

The eigenvectors and eigenvalves of a matrix

fully characterize its properties. For the matrix representing the Isaacs assumptions the following eigenvalues (λ's) and eigenvectors ($\bar{u}$'s) can be obtained:

$$\lambda_1 = 1 \qquad \lambda_2 = K_1 + K_3 \qquad \lambda_3 = 0$$

$$u_1 = \begin{pmatrix} 1 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_2 = \begin{pmatrix} 0 \\ \frac{K_1}{K_2} \\ \frac{K_3}{K_2} \end{pmatrix} \quad u_3 = \begin{pmatrix} 0 \\ 1 \\ -1 \end{pmatrix}.$$

Any initial state of the system (e.g., $\bar{w}$) can be written as a weighted sum of the eigenvectors

$$\bar{w} = c_1\bar{u}_1 + c_2\bar{u}_2 + c_3\bar{u}_3.$$

If we now apply A n times to this vector we obtain

$$A^n\bar{w} = c_1\lambda_1^n\bar{u}_1 + c_2\lambda_2^n\bar{u}_2 + c_3\lambda_3^n\bar{u}_3.$$

After a sufficient time (n very large), the second and third term will vanish, leaving an expression for the final state of the system:

$$\lim_{n\to\infty} A^n\bar{w} = c_1\bar{u}_1.$$

In Isaacs' terms $c_1 = M_0$ and the limiting values for the second and third compartments are M'_t and M''_t respectively. Therefore

$$M'_t = M_0K_1/K_2$$
$$M''_t = M_0K_3/K_2$$

which is exactly Isaacs' result.

For the nine constant model, there is also always a steady state distribution of matter in the system. By finding the eigenvector corresponding to an eigenvalue of one, we can obtain the following steady state values of M'_t (total quantity of material in living matter) and M''_t (total in nonliving recoverable material) in terms of a constant input M_0:

$$M'_t = \frac{-k_1(k_8-1) + k_2k_7}{(k_4-1)(k_8-1) - k_5k_7} M_0$$

$$M''_t = \frac{-k_2(k_4-1) + k_5k_1}{(k_4-1)(k_8-1) - k_5k_7} M_0.$$

Trophic Level Equations

In addition to values for total amounts of living and retrievable dead matter, Isaacs develops equations for general trophic levels. His equations can be generated by our approach if our original matrix is broken down into component parts and then applied to the steady state vector. For example, let us consider Isaacs' case (Isaacs 1973) of a subset of trophic levels which are complete and mutually exclusive. He considers strict herbivores, detrital feeders, and full predators to be such a subset.

Our original matrix A can be written in the following way

$$A = A_{S+R} + A_H + A_D + A_P$$

where

$$A_{S+R} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 0 \\ K_3 & K_3 & K_3 \end{pmatrix}$$

$$A_H = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_D = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & K_1 \\ 0 & 0 & 0 \end{pmatrix}$$

$$A_P = \begin{pmatrix} 0 & 0 & 0 \\ 0 & K_1 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

A_{S+R} = matrix responsible for the biomass in source and the retrievable dead matter,
A_H = matrix responsible for biomass in herbivores,
A_D = matrix responsible for biomass in detrital feeders, and
A_P = matrix responsible for biomass in predators.

To obtain the potential biomass for each of the trophic levels, we take the appropriate matrix times the steady state vector. Thus, the equation for the potential biomass of herbivores is obtained from

$$A_H\bar{u}_1 = \begin{pmatrix} 0 & 0 & 0 \\ K_1 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} M_0 \\ \frac{M_0K_1}{K_2} \\ \frac{M_0K_3}{K_2} \end{pmatrix} = \begin{pmatrix} 0 \\ M_0K_1 \\ 0 \end{pmatrix}.$$

Similarly, for detrital feeders

$$A_D \bar{u}_1 = \begin{pmatrix} 0 \\ \dfrac{M_0 K_1 K_3}{K_2} \\ 0 \end{pmatrix}$$

and for predators

$$A_P \bar{u}_1 = \begin{pmatrix} 0 \\ \dfrac{M_0 K_1^2}{K_2} \\ 0 \end{pmatrix}.$$

All of Isaacs' other equations for trophic level potential biomasses or fluxes can be obtained in a similar manner.

Equations for the potential biomass of trophic levels can also be calculated for the generalized model. This is done in a manner similar to that described in the previous section.

Strict herbivores (feeding on source):

$$M_m = M_0 k_1.$$

Omnivores (feeding on source, living and retrievable dead):

$$M_v = M_0 \left(\frac{-k_1 (k_8 - 1) + k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_1 M_0 + k_4 M'_t + k_7 M''_t.$$

Particle feeders (feeding on source and retrievable dead):

$$M_\mu = M_0 \left(\frac{k_1 (k_4 - 1)(k_8 - 1) + k_2 k_7 (1 - k_4)}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_1 M_0 + k_7 M''_t.$$

Detrital feeders (feeding on retrievable dead):

$$M_d = M_0 \left(\frac{-k_2 k_7 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_7 M''_t.$$

Full predators (feeding on living):

$$M_P = M_0 \left(\frac{-k_4 k_1 (k_8 - 1) + k_4 k_2 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_4 M'_t.$$

Nonherbivorous omnivores (feeding on living and retrievable dead):

$$M_n = M_0 \left(\frac{-k_4 k_1 k_8 + k_1 k_4 + k_2 k_7 + k_1 k_5 k_7}{(k_4 - 1)(k_8 - 1) - k_5 k_7} \right)$$

$$= k_4 M'_t + k_7 M''_t.$$

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DISTRIBUTION AND ECOLOGY OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, IN AN OFFSHORE AREA OF THE EASTERN TROPICAL PACIFIC OCEAN

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ABSTRACT

Distributions of skipjack tuna, *Katsuwonus pelamis*, were studied in the offshore eastern tropical Pacific between lat. 15°N and 5°S, long. 115° and 125°W, during two cruises in 1970 and 1971. Another cruise was made there with different methods in 1969. All cruises were between October and April. Various environmental properties were measured.

Catches of skipjack included fish smaller and larger than those generally taken near the American coast. This is consistent with previous hypotheses that mature adults and their larvae generally occur far offshore, whereas adolescents are generally coastal, in the eastern Pacific. The juveniles arriving near the coast and the older fish leaving it evidently cross the studied area on migrations from and to the spawning regions.

In 1970 and 1971 skipjack > 45 cm were most abundant in the equatorial upwelling and at the northern boundary of the North Equatorial Countercurrent, and scarce in the Countercurrent. Correlation coefficients between skipjack > 45 cm and skipjack forage in 1970 were positive and significant by the usual criteria, but the significance may in part be disputable because many other correlations involving skipjack were nonsignificant. The apparent significance was lost when juvenile skipjack (< 45 cm) were included with the larger ones. Juveniles may have different relations to environment. The 1971 data were scanty and yielded no significant correlations between skipjack and forage.

On the 1969 cruise forage was not studied. Skipjack were abundant in the Countercurrent, but at a prespawning stage, whereas postspawners predominated on the other cruises. Other studies suggest that skipjack larvae require relatively high temperatures, which occurred only in the Countercurrent on the 1969 cruise. Skipjack may be distributed according to the environmental requirements of their larvae when spawning and according to their own feeding requirements when not spawning.

Williams (1971) described plans for a series of cruises in two offshore areas of the eastern tropical Pacific Ocean. This report deals with results of two cruises made in 1970 and 1971 in one of the areas, bounded by lat. 15°N-5°S and long. 115°-125°W (Figure 1). The cruises were initiated by the National Marine Fisheries Service, Southwest Fisheries Center, and the Scripps Tuna Oceanography Research (STOR) Program, Institute of Marine Resources, University of California. They were designed to investigate on a seasonal basis the occurrence and relative abundance of skipjack tuna, *Katsuwonus pelamis*, in relation to environmental conditions. Coverage of

FIGURE 1.—Area of eastern tropical Pacific Ocean under investigation.

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offshore areas by the U.S. surface tuna fishery has been very limited, especially for skipjack. Coverage by the Japanese subsurface tuna fishery has been greater, but still poor for skipjack (Miyake 1968). The regulation of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific is expected to increase the need for information on skipjack in the offshore waters.

Work in coastal waters has shown that adult skipjack are most numerous when temperature is in the range 20° to 29°C (Williams 1970) and standing stock of skipjack forage is high (Blackburn 1965, 1969). Sea surface temperatures are in the suitable range for most of the year throughout the offshore eastern tropical Pacific (Wyrtki 1964; La Violette and Seim 1969; Love 1971b, 1972a, b, in prep.). Thus distribution of forage seemed likely to be a main factor in determining distribution of adult skipjack in offshore waters. The distribution of forage in that region was described from data of EASTROPAC Expedition (1967-68) by Blackburn and Laurs (1972), who expected that adult skipjack would prove to be distributed in the same way. One of the purposes of the present study was to test that expectation. The forage concentrations on EASTROPAC were characteristically high in certain zones of latitude and low in others, broadly corresponding to distributions of phytoplankton, zooplankton, and total micronekton (Love 1970, 1971a, in prep.; Blackburn et al. 1970; Owen and Zeitzschel 1970a).

Evidence, summarized by Williams (1972), indicates that most exploited skipjack in the eastern Pacific have a spawning origin in the central Pacific west of long. 130°W. It also suggests that the majority of the skipjack enter the present fishery, which is concentrated near tropical American coasts, during only 1 yr of their life history. They are then relatively small (average length about 50 to 55 cm, average weight 3 to 3.5 kg) and sexually immature. Thus it is probable that migration pathways exist for skipjack, both below and above these sizes, across the offshore eastern tropical Pacific.

Such pathways might occur at particular latitudes since forage concentrations and many other ocean conditions, including surface currents, are zonally oriented. On this basis Williams (1972) presented three qualitative models of the migration of young (recruit) skipjack from the central Pacific into the eastern Pacific fishing areas. The data from the present cruises may be useful for testing and modification of the models, and incorporation with other models of skipjack movement such as that of Seckel (1972).

PLAN OF THE INVESTIGATIONS

The inward skipjack migration models of Williams (1972) assumed that the routes were principally zonal across the offshore eastern Pacific. Mechanisms and timing of the migrations are probably dependent on oceanographic conditions and events in this region. The strategy for the present investigations was to have latitudinal sampling of fish and environmental parameters in meridional areas considered critical to the migrations. The area discussed in this paper includes the meridian of 119°W. It is important because the surface North Equatorial Countercurrent normally becomes intermittent or absent east of this meridian from January to May.

Each cruise had two parts (Williams 1971). Part I was a rapid meridional transect of the area along long. 119°W to monitor ocean conditions and compare them with previous data. These results showed the positions of zonal surface current boundaries and forage bands, and hence the latitudinal zones that were to be fished for skipjack.

In Part II detailed fisheries operations were carried out in the selected zones to a standardized plan based on a "unit area" of 2° latitude by 2° longitude, together with supporting environmental observations. Fishing was by multiple trolling during daylight. Figure 2 shows schematically the track and scheduled observations. The work time for each unit area, including entry and exit, was 96 h. Coverage in a zone of latitude could consist of any multiple of unit areas or fractions thereof (quadrants or 1° × 1° areas).

The first cruise in November-December 1970 utilized the vessels *Townsend Cromwell* (Cruise C 51) (R. Uchida, Chief Scientist) and *David Starr Jordan* (J 57) (F. Williams, Chief Scientist). The second cruise in March-April 1971, was made with only the *Jordan* (J 60) (M. Blackburn, Chief Scientist). The *Jordan* 60 cruise was severely curtailed due to illness of a crew member. On the first cruise the Part I transect was completed by the *Cromwell*; and data were sent by radio to the *Jordan*; subsequent Part II operations were carried out by both vessels.

This paper also discusses data from a cruise made by National Marine Fisheries Service, Hawaii, to the same area in October-November

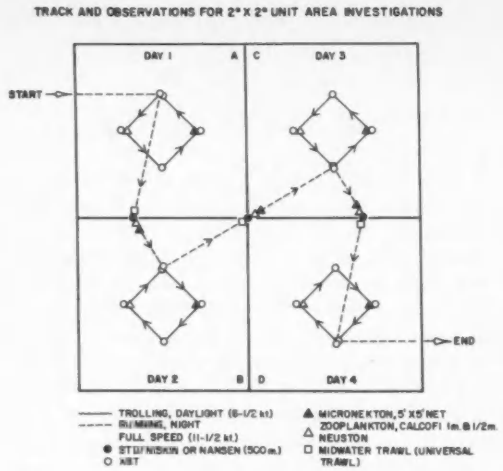


FIGURE 2.–Track and observations scheduled for each 2° × 2° unit area during Part II operations. [Dawn trawl haul was eliminated on cruise *Jordan* 60].

1969, in more detail than the previous cruise report by Hida (1970).

METHODS

This section deals with methods used on the 1970 and 1971 cruises. The Bissett-Berman[3] Salinity-Temperature-Depth probe (STD) and Sippican expendable bathythermograph (XBT) were used for measuring temperature and salinity. A Niskin 12-bottle rosette sampler coupled with the STD was used to collect water samples for salinity and oxygen. The STD system had digital (magnetic tape data logger) and analog chart outputs, as did the XBT system (punched paper tape and analog chart). STD/Niskin casts were normally made to 500 m and XBT drops to 450 m. Nansen bottle casts, for calibration of the STD system, were made at the start and finish of the Part I transect and at intervals during Part II fishing operations. On the Part I transect, STD/Niskin stations for temperature, salinity, and oxygen were made every 6 h, with one or more XBT drops between STD stations. In Part II operations, three STD stations were made at night in each 2° × 2° unit area, and five XBT drops between dawn and dusk on fishing tracks (Figure 2). Processing of the physical oceanographic data was as described by Taft and Miller (1970). Depth of the mixed layer was derived directly from analog charts of XBT and STD systems according to criteria of Owen (1970a).

Dissolved oxygen content of water samples from the Niskin sampler was determined, and data processed, as indicated by Owen (1970b). Discrete surface samples for chlorophyll *a* were taken at approximately noon and midnight and processed as described by Owen and Zeitzschel (1970b).

Zooplankton hauls were made and samples processed by the methods used on EASTROPAC Expedition (Laurs 1970). Oblique hauls from 200 m to surface were made with nets of 50 cm and 1 m mouth diameter in a paired frame. A wire angle of 45° was maintained during the haul at a speed about 1.5 to 2 knots. In Part II operations, one daylight haul was made during each of 4 days of fishing in a 2° × 2° unit area (see Figure 2), and three night hauls were made during the 4-day period. No hauls were made near dawn or dusk. Data were expressed in displacement volume in milliliters per 1,000 m^3.

Micronekton was sampled with a net 1.5 m square at the mouth, in oblique hauls from 200 m to surface at a ship speed of 5 knots (Blackburn 1968, 1970; Blackburn et al. 1970). During the Part I transect, micronekton hauls were made at approximately 12-h intervals following STD casts, one during daylight and one at night. In Part II operations, day and night hauls were made with the same frequency as for zooplankton (see Figure 2). Processing of the samples and estimation of volume of water strained was as discussed by the same authors, and total micronekton was expressed as displacement volume in milliliters per 1,000 m^3. A variable and generally large proportion of this micronekton consisted of organisms that skipjack are known or likely to eat (skipjack forage) in the eastern tropical Pacific. The micronekton catches were therefore sorted into forage and nonforage organisms (Blackburn and Laurs 1972). Forage organisms were all crustaceans, all cephalopods, all epipelagic fish and *Vinciguerria*. Nonforage organisms were all mesopelagic fish except *Vinciguerria* and all leptocephali.

The trolling gear used to catch skipjack and other fish was similar to that used in the albacore fishery off the U.S. west coast (Yoshida 1966). Feather jigs were fished with nylon traces and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

nylon parachute cord lines. The *Cromwell* could fish only 4 lines from the stern, compared with 11 fished by the *Jordan*, 8 from outriggers and 3 from the stern. On the *Jordan* the 4 lines on each outrigger were connected to a set of hydraulic power gurdies for rapid hauling.

Charts and sections were contoured by hand except those of dissolved oxygen content which were prepared by computer and Calcomp plotter. Gear and methods used for neuston and midwater trawl samples are not discussed because the results are not utilized in this report. The same applies to observations on birds, fish schools, and marine mammals.

RESULTS OF THE EXPERIMENTAL FISHING

Based on the position of the surface current boundaries and distributions of temperature and skipjack forage derived from Part I operations, the latitudinal zones investigated in Part II fishing operations were similar on the 1970 and 1971 cruises: 12°-14°N, 9°-11°N, 6°-8°N, 3°-5°N, 1°-3°N, and 2°-4°S. Figures 3 and 4 show the cruise tracks during Part II fishing operations in the above-mentioned zones. They also show approximate positions of surface current boundaries, which were obtained from data on thermocline topography.

The total fishing effort (number of line-hours) in or immediately adjacent to the study area was very much higher on the November-December 1970 cruise than in March-April 1971, because of the curtailment of the latter cruise (Table 1). The catch by species on each cruise is given in Table 2, which shows the number boarded and kept, tagged and released, and lost but identified, and the overall size range of each species. Skipjack was obviously the dominant species on each cruise.

TABLE 1.–Total fishing effort in the study area.

Period	Cruise no.		Line-hours fished	
			in unit areas	on passage
Nov.-Dec. 1970	*Jordan* 57	2,746	3,213	131
Nov.-Dec. 1970	*Cromwell* 51	467		
Mar.-Apr. 1971	*Jordan* 60		2,088	255

DISTRIBUTION AND RELATIVE ABUNDANCE OF SKIPJACK AND OTHER TUNA

This section deals with results from the 1970 and 1971 cruises. Relative abundance of skipjack was calculated in terms of catch per line-hour on track. Catch equals number boarded, tagged, and lost but identified. Fish taken when the vessel circled following an initial strike, or when chumming with live anchovy, are not included. Troll catches of skipjack made on track and separated, arbitrarily, by >10 min are considered to have come from separate schools or aggregations of fish, and an index of schools encountered per hour of trolling has been derived. There are highly significant positive correlations between catch/line-hour and schools/hour for each cruise ($r = +0.907$ for data of Table 3 and $+0.716$ for Table 4, both significant at the 1% level). Schools/hour is a more conservative indicator of relative abundance of skipjack than catch/line-hour because each

TABLE 2.–Summary of fish catch by species: Cruises *Jordan* 57-*Cromwell* 51, November-December 1970, and *Jordan* 60, March-April 1971.

Species	*Jordan* 57-*Cromwell* 51				*Jordan* 60			
	Boarded	Tagged	Lost but identified	Size range (cm)	Boarded	Tagged	Lost but identified	Size range (cm)
Skipjack *(Katsuwonus pelamis)*	114	67	~418	32.5- 71.0	61	8	49	41.8-70.0
Yellowfin tuna *(Thunnus albacares)*	30	4	5	26.2-111.5	2	–	–	33.5-44.7
Frigate mackerel *(Auxis thazard)*	2	–	–	30.2- 31.0	1	–	–	34.6
Unidentified tuna	–	–	12	–	–	–	–	–
Wahoo *(Acanthocybium solandri)*	4	–	1	52.0-110.0	–	–	–	–
Shortbill spearfish *(Tetrapturus angustirostris)*	–	–	1	–	–	–	–	–
Dolphin *(Coryphaena hippurus)*	8	–	–	20.5-114.5	6	–	~5	34.0-46.3
Pompano dolphin *(C. equiselis)*	4	–	2	26.5- ~50.0	–	–	–	–
Rainbow runner *(Elagatis bipinnulatus)*	–	–	–	–	1	–	–	81.5
Unidentified fish (lost)	–	–	10	–	–	–	10	–

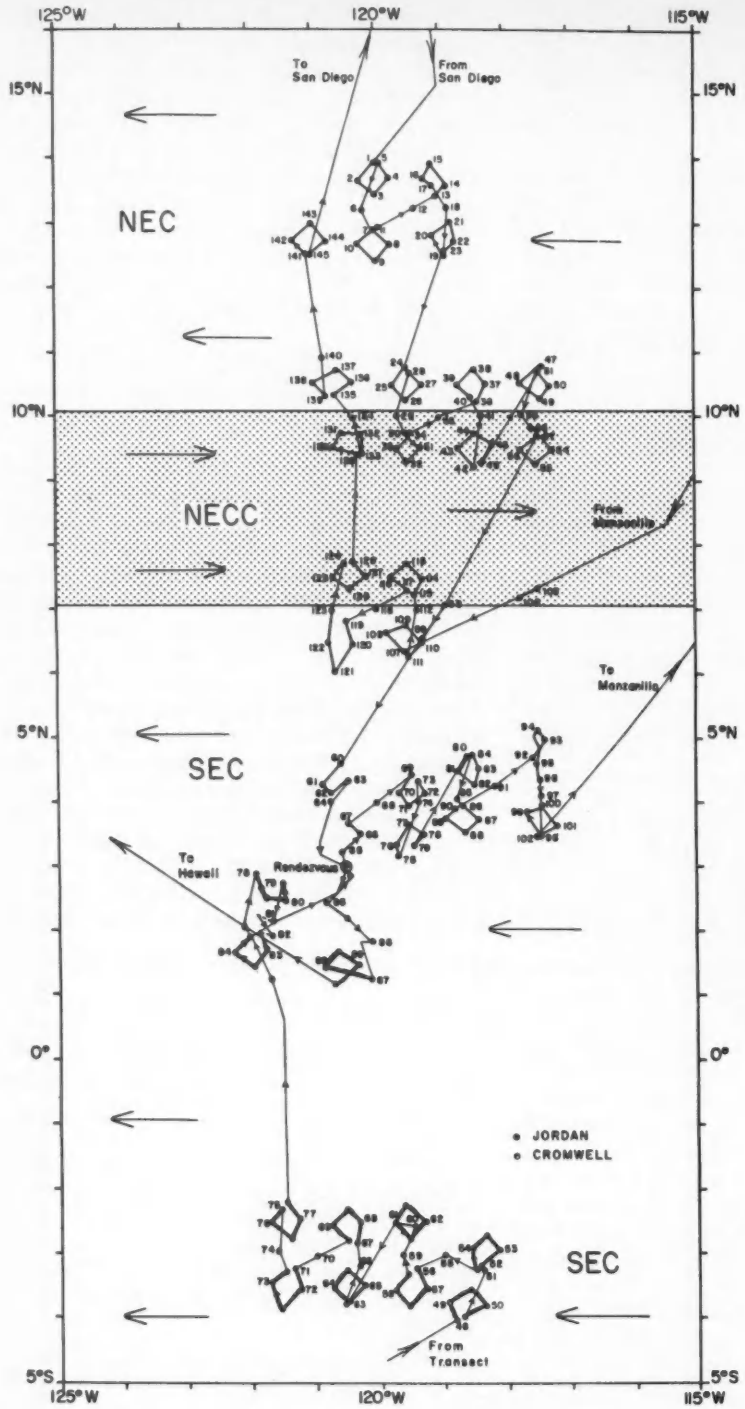


FIGURE 3.—Cruise tracks, Part II operations, *Jordan 57-Cromwell 51*, November-December 1970. Thickened lines indicate daylight fishing tracks. Approximate boundaries of surface currents are indicated.

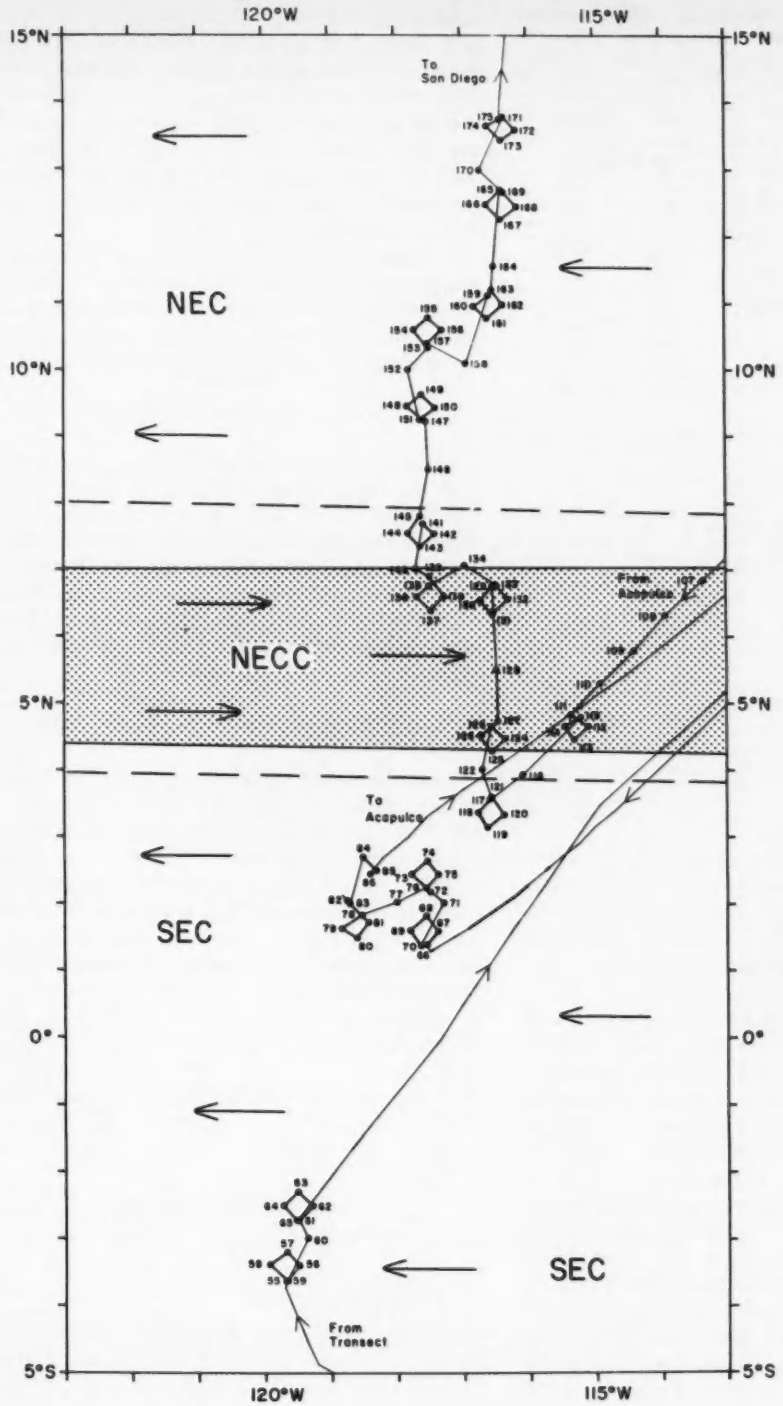


FIGURE 4.—Cruise tracks, Part II operations, *Jordan* 60, March-April 1971. Thickened lines indicate daylight fishing tracks. Approximate boundaries of surface currents are indicated.

TABLE 3.—Relative abundance of troll-caught skipjack and other tuna, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Zone latitude	Current system	Catch/line-hour			Schools/hour skipjack
		Skipjack	Yellowfin	All tuna	
13°-14°N	NEC	0.072	0	0.072	0.10
12°-13°N	NEC	0.038	0.057	0.101	0.17
10°-11°N	NEC	0.064	0.022	0.099	0.17
9°-10°N	NECC	0.014	0	0.014	0.08
7°-8°N	NECC	0.075	0.004	0.079	0.10
6°-7°N	SEC	0.009	0	0.037	0.05
4°-5°N	SEC	0.100	0	0.100	0.10
3°-4°N	SEC	0.130	0.016	0.146	0.25
2°-3°N	SEC	0.015	0	0.015	0.06
1°-2°N	SEC	0.354	0	0.354	0.40
0°40′-1°N[1]	SEC	0.208	0	0.208	0.48
2°-3°S	SEC	0.096	0	0.096	0.13
3°-4°S	SEC	0.028	0	0.028	0.10

[1]Data on this line are from fishing on passage, <50 line-h.

TABLE 4.—Relative abundance of troll-caught skipjack and other tuna, Cruise *Jordan* 60, March-April 1971. Data in square brackets are from fishing on passage and are included in totals to the left.

Zone latitude	Current system	Catch/line-hour			Schools/hour skipjack
		Skipjack	Yellowfin	All tuna	
[16°-17°N	NEC	0.064	0	0.064	0.32]
13°-14°N	NEC	0.008	0.008	0.016	0.09
12°-13°N	NEC	0.054	0	0.054	0.08
10°-11°N	NEC	0.107	0	0.107	0.46
9°-10°N	NEC	0.134	0	0.134	0.17
7°-8°N	NEC	0	0	0	0
6°-7°N	NECC	0.031	0	0.031	0.09
4°-5°N	NECC/SEC	0.042	0.004	0.046	0.08
3°-4°N	SEC	0	0	0	0
2°-3°N	SEC	0.023 [0.019]	0	0.023 [0.019]	0.12 [0.10]
1°-2°N	SEC	0.067 [0.064]	0	0.067 [0.064]	0.17 [0.17]
2°-3°S	SEC	0.062	0	0.063	0.25
3°-4°S	SEC	0.039	0	0.029	0.16

aggregation is given equal weighting irrespective of the number of fish caught. The index does not reflect the size of the aggregations, which on both cruises were considered to be relatively small. No large surface schools of skipjack or other tuna were seen in the study area.

Tables 3 and 4 show the relative abundance of skipjack, yellowfin tuna and total tuna as catch/line-hour and skipjack as schools/hour for 1° latitudinal zones fished in Part II operations. Approximate boundaries of surface current systems are also indicated: NEC, NECC, and SEC mean North Equatorial Current, North Equatorial Countercurrent, and South Equatorial Current. In November-December 1970 the highest level of relative abundance of skipjack was between lat. 0°40′ and 2°N, with a secondary maximum at lat 3° to 5°N and other high levels north of the NECC and south of the Equator. Within the NECC at lat. 7° to 10°N, relative abundance in terms of catch rate was variable, but generally low in terms of schools encountered. With the added contribution of yellowfin and other tuna, there was a marked maximum north of the NECC. In March-April 1971, overall relative abundance was much lower, and the principal maximum was situated north of the NECC, between lat. 9° and 11°N. Secondary maxima occurred at lat. 1° to 3°N and south of the Equator. The relative abundance of skipjack in the NECC was again low.

In Figures 5, 6, 7, and 8, daily values of relative abundance (catch rates and schools) are plotted and contoured. The results are more difficult to interpret in this form, but there are some general agreements with the zonally averaged data.

Off-track Catches of Skipjack

Off-track troll catches of skipjack were made with the use of anchovy, *Engraulis mordax*, live bait on *Jordan* 57. On five occasions schools of skipjack were chummed with live bait, following initial jig strikes (4) or fish sighting (1). On two of these occasions the chumming and circling of the vessel produced a substantial additional catch. Use of live bait on cruises of this type is advantageous in order to increase sample size of fish.

Distribution of Skipjack by Time of Day

Percentages of the total numbers of skipjack schools encountered on track in each 1-h period have been calculated and are given in Table 5. Schools are defined as above. Some 60-min periods included station time (i.e., not fishing), and the numbers of schools per unit time have been adjusted. Variability in occurrence is considerable between cruises for 1-h periods. However, when presented by 2-h periods, the temporal occurrence of skipjack shows remarkable similarity on the two cruises. Surprisingly, fewest aggregations were encountered before 1000 h. Aggregations were encountered most frequently between 1200 and 1500 h, and again, as expected, in the predusk period, 1700 to 1759 h.

Biological Characteristics of Skipjack and Other Tuna

Size of Skipjack

Measurements of fish length (tip of snout to tip of median caudal fin rays) were made to the nearest millimeter on all fish. Table 6 shows the

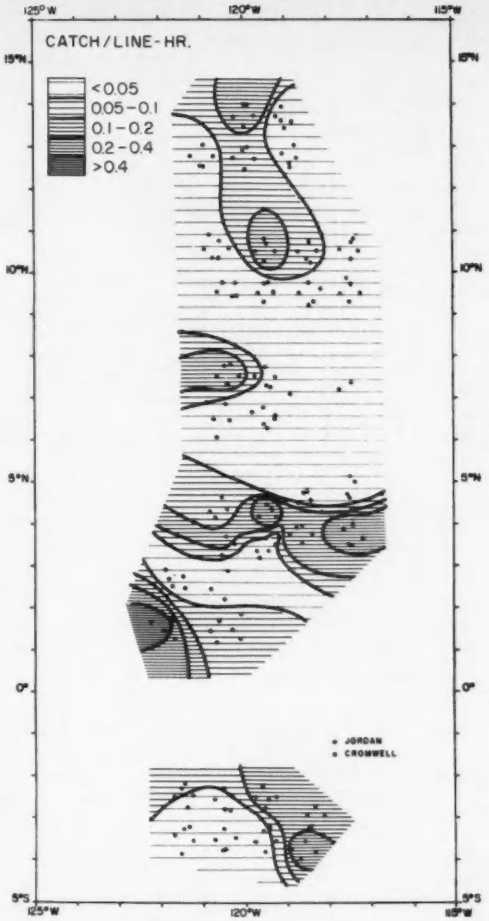


FIGURE 5.—Relative abundance of skipjack in catch/line-hour, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

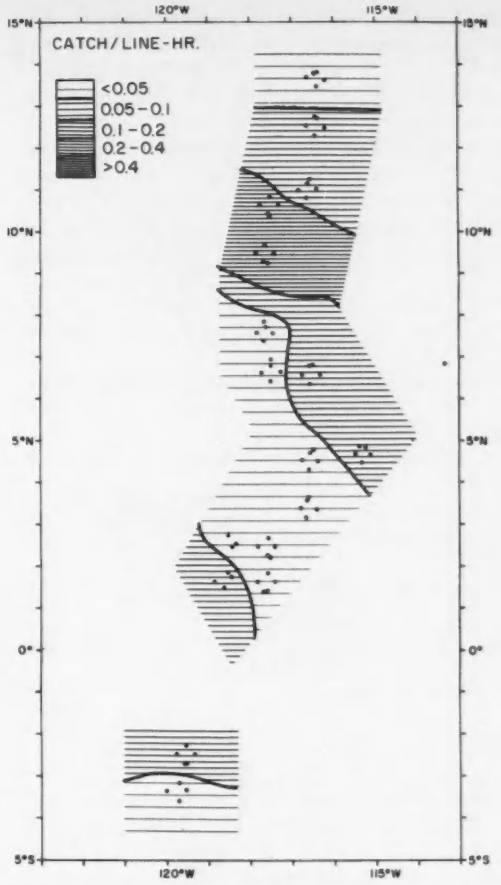


FIGURE 6.—Relative abundance of skipjack in catch/line-hour, cruise *Jordan* 60, March-April 1971.

percent of skipjack in three broad size categories for the two cruises. The most significant feature is that 13.3% of skipjack were <45 cm in November-December 1970, as against 2.9% on the next cruise.

The fish <45 cm were not distributed over a large part of the area, as fish >45 cm were, in November-December 1970. Of the small fish, 16 (85%) were from areas north of the NECC, lat. 10° to 14°N, and the remaining 3 (15%) from south of the NECC, lat. 0°30′ to 4°N; none were found in the NECC or south of the equator. Table 7 shows small skipjack (<45 cm) as percent of total in the latitudinal zones north of 10°N. It appears that the

TABLE 5.—Percent[1] of total number of skipjack schools encountered on track, by 1-h periods (all fishing days combined): Cruises *Jordan* 57-*Cromwell* 51, November-December 1970, and *Jordan* 60, March-April 1971.

Time period	*Jordan* 57-*Cromwell* 51		*Jordan* 60	
Start[2]-0659	3.7%	12.3%	12.2%	12.2%
0700-0759	8.6		0	
0800-0859	2.5	9.4	3.6	9.4
0900-0959	6.9		5.8	
1000-1059	8.8	16.0	10.6	16.2
1100-1159	7.2		5.6	
1200-1259	14.9	21.2	2.9	20.2
1300-1359	6.3		17.9	
1400-1459	7.5	14.8	15.8	21.6
1500-1559	7.3		5.8	
1600-1659	7.3	26.3	5.4	19.8
1700-1759	19.0		14.4	
Total fishing days	28		21	

[1]Adjusted data, see text p. 388.
[2]Mean start 0556 h and 0539 h on *Jordan* 57-*Cromwell* 51 and *Jordan* 60 respectively.

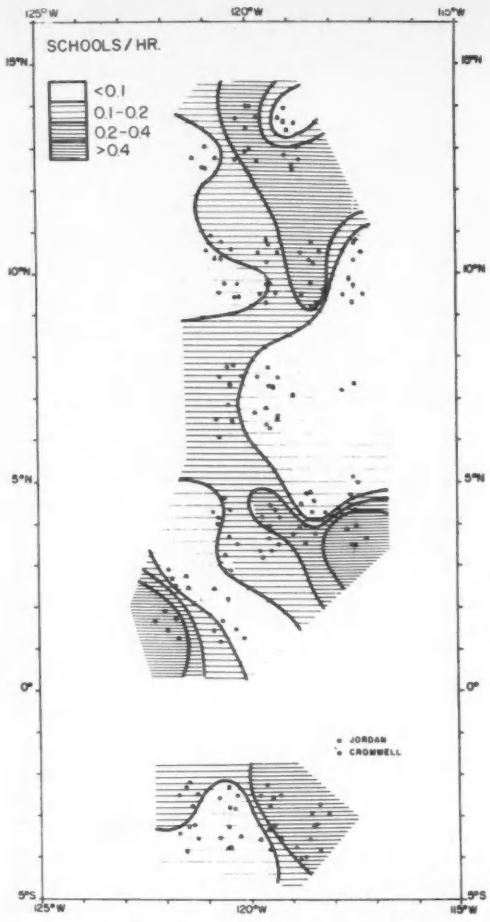


FIGURE 7.—Relative abundance of skipjack in schools/hour, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

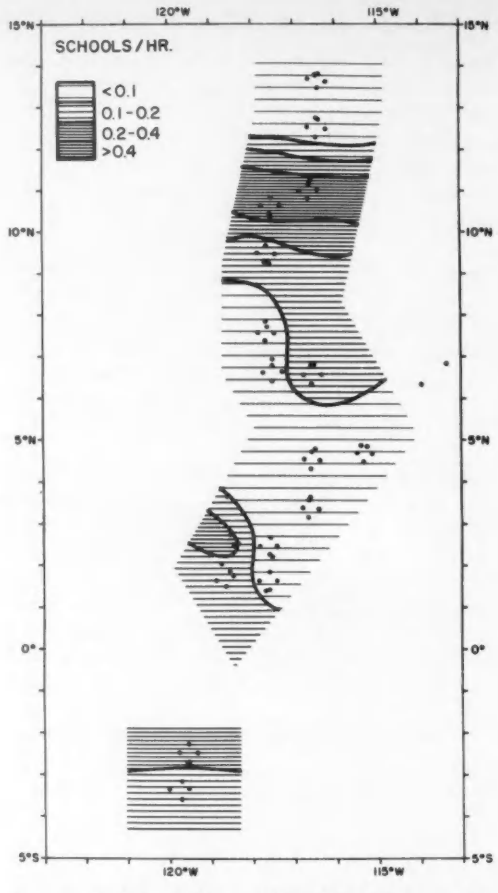


FIGURE 8.—Relative abundance of skipjack in schools/hour, cruise *Jordan* 60, March-April 1971.

fish < 45 cm were largely segregated geographically from the medium and large ones. Figure 9 indicates a distinct separation in age as well. Small skipjack were very scarce in March-April 1971.

Figure 9 shows the percent length-frequency distributions of skipjack by 2-cm classes. In November-December 1970, the principal mode was at 58 cm, with a minor mode at 36 cm and perhaps another at 48 cm. The fish of modal size 36 cm could be about 14 to 15 mo old, if one accepts the growth rates for juveniles indicated by Yoshida (1971) and Joseph and Calkins (1969: from tagging data, averaged). This would suggest a spawning origin in the northern summer. Because no definite information is available on skipjack growth rates beyond this size, the age represented by the 58-cm mode is uncertain, but probably it is 2 to 3 yr. Whether the possible mode at 48 cm represents fish 1 yr or 6 mo between the other two modes is not known. If there were 6-mo difference, it would signify a spawning origin in the southern summer.

In March-April 1971, there is a single wide mode composed of fish > 48 cm (peak 56 to 60 cm). The fish had about the same size distribution in all areas.

Skipjack in the eastern Pacific coastal fishery ranged from about 3 to 3.5 kg, with mean and modal lengths 50 to 55 cm, in the years 1955-71 (Miyake 1968; Inter-American Tropical Tuna

TABLE 6.–Skipjack in size categories as percent of total, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970 and *Jordan* 60, March-April 1971.

Size (cm)	Percent of total	
	Jordan 57-*Cromwell* 51	*Jordan* 60
<45	13.3	2.9
45-60	62.2	55.1
>60	24.5	42.0
Total skipjack	143	70

TABLE 7.–Small skipjack (<45 cm) as percent of total in latitudinal zones north of 10°N, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Zone latitude	Size (cm)			No. of fish	Percent
	Category	Range	Mean		
12°-14°N	<45	32.5-39.8	35.5	13	76.5
	>45	48.8-56.5	54.2	4	23.5
10°-11°N	<45	33.4-34.7	34.2	3	13.6
	>45	45.0-65.0	58.0	19	86.4

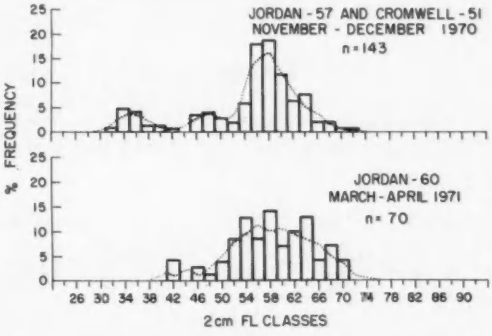


FIGURE 9.–Skipjack percent-length-frequency distribution in the study area. Smoothed curves are from 3-figure moving averages. Stated length indicates midpoint of class.

Commission 1966, 1972). The principal component of the Hawaiian catch usually consists of fish of modal sizes >60 cm (U.S. Bureau of Commercial Fisheries 1963; Rothschild 1965; Higgins 1966). The principal modes of skipjack caught in the study area, 56 to 60 cm on the two cruises, are intermediate between those in the eastern Pacific coastal fishery and the Hawaiian fishery. Purse seine samples of skipjack obtained in and near the study area in 1970 and 1971, which are mentioned later, had mean sizes from 58 to 61 cm.

Size of Other Tuna

Only 34 yellowfin tuna were boarded (39 caught) on the November-December 1970 cruise, and 2 in March-April 1971. None were taken south of lat. 3°N. Yellowfin ranged from 26 to 112 cm, with mean lengths for different aggregations ranging from 28.5 to 42.3 cm. The majority (68%) were <45 cm. These small yellowfin were mainly (83%) from the same latitudinal zone (10°-14°N) as the small skipjack. On three occasions schools of mixed small tunas–skipjack, yellowfin, and frigate mackerel (*Auxis*: 30 to 31 cm)–were sampled north of lat. 10°N. Small tuna of different species may occur together because of similar environmental and food requirements, and behavior.

Sex and Maturity of Skipjack

Sex ratios of skipjack for the two cruises were as follows:

November-December 1970: Total 143, Sexed 72

Males 24; females 33; indeterminate 15

Ratio: Males to females, 1:1.4

March-April 1971: Total 72, sexed 59

Males 24; females 35

Ratio: Males to females, 1:1.5

Gonad maturity was determined macroscopically in the field, and stages were classified as follows:

Immature, virgin	Roughly	1 - S
Immature, resting	equivalent	1
Maturing	to indicated	2
Spent	stages in	5 - A
Spent-recovering	Orange (1961)	5 - B

The number of gonads in each stage by size of fish are given in Tables 8 and 9.

In November-December the smallest spent or spent recovering female skipjack was 46.5 cm. In March-April the corresponding size for females was 49.8 cm, and for males 48.3 cm. These data support other evidence that first maturity in female skipjack in the Pacific is reached between 40 and 45 cm (Orange 1961; Waldron 1963; Kawasaki 1965).

A relatively large number of recently spawned fish, i.e., with spent and spent-recovering gonads, was taken on each cruise: 30% of the females and 7% of the males in November-December 1970, and

TABLE 8.—Number of skipjack gonads in each maturity stage by size of fish, Cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

Size class (cm)	Immature: Virgin M	Immature: Virgin F	Immature: Resting M	Immature: Resting F	Maturing M	Maturing F	Spent M	Spent F	Spent recovering M	Spent recovering F
<40	?	15	?							
40-49.9		1	5	1						1
50-59.9			5	12	1			1	2	6
60-69.9			11	2		2				
≥70								2		

Totals: males (M) 24; females (F) 28; indeterminate (<40 cm) 15.

TABLE 9.—Number of skipjack gonads in each maturity stage by size of fish, Cruise *Jordan* 60, March-April 1971.

Size class (cm)	Immature: Virgin M	Immature: Virgin F	Immature: Resting M	Immature: Resting F	Maturing M	Maturing F	Spent M	Spent F	Spent recovering M	Spent recovering F
<40										
40-49.9				2					1	1
50-59.9			5	1	1				10	13
60-69.9					2	8			5	8
≥70						1				

Totals: males (M) 24; females (F) 34.

63% and 67%, respectively, in March-April 1971 (Tables 8, 9). Most others were at the immature resting stage. The spent-recovering fish appeared to be at a more advanced stage of recovery in March-April than in November-December 1970.

Data on other skipjack ovaries taken from or near the study area in 1970-71 are available from samples of purse seine-caught fish examined by the Inter-American Tropical Tuna Commission (C. L. Petersen, pers. commun.). Gonad indices were calculated by them according to Orange (1961), and data are given in Table 10.

The principal interest lies in the samples (mean lengths >57 cm) from long. 110°W westwards. It is assumed that gonad indices < 15.1 indicate immature (virgin or resting) or spent-recovering ovaries, 15.1 to 45 indicate maturing ovaries, and > 45 indicate mature or ripe ovaries. The occurrence of 35% of skipjack ovaries with indices > 45 in the middle of the study area in September 1970 may correspond to the 36% of ovaries in spent condition in fish >50 cm in the same area in November-December 1970 (Table 8). The sample from lat. 5°N, long. 110°W in April 1971 (Table 10) showed similar ovarian states to those in skipjack > 50 cm caught in March-April 1971 (Table 9): about 75% immature or spent-recovering, and 25% maturing, in each case.

Sex and Maturity of Yellowfin

In November-December 1970, 24 specimens of yellowfin under 50 cm were classified as immature, sex indeterminate; of 5 yellowfin from 50 to 60 cm, 3 were immature female, 1 was immature male, and 1 was indeterminate.

OBSERVATIONS ON THE ENVIRONMENT IN RELATION TO SKIPJACK

Temperature

The data from Part I operations on the 1970 and 1971 cruises were used to construct temperature

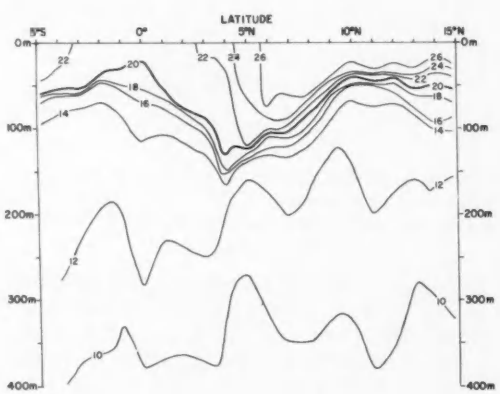


FIGURE 10.—Temperature (°C) section from lat. 15°N to 5°S along long. 119°W, cruise *Cromwell* 51, 1-7 November 1970.

TABLE 10.—Gonad indices of female skipjack caught by purse seine in northeastern tropical Pacific, 1970-71.

Date of capture	Approximate position: Lat. °N	Approximate position: Long. °W	Gonad indices: % <15.1	Gonad indices: %15.1-45	Gonad indices: % >45	Sample no.	Size (cm): Range	Size (cm): Mean
23 August 1970	5	135	48.9	46.8	4.3	50	53.5-63.8	59.9
8 September 1970	5	120	2.5	62.5	35.0	40	55.0-62.3	57.8
April 1971	5	110	76.0	24.0	0	50	54.3-67.6	60.5
30 April 1971	5	90	57.1	42.9	0	49	53.3-68.7	62.3
May 1971	5	90	32.0	60.0	8.0	59	57.8-70.0	64.5

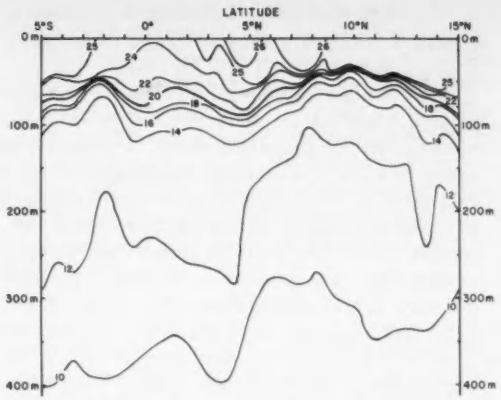
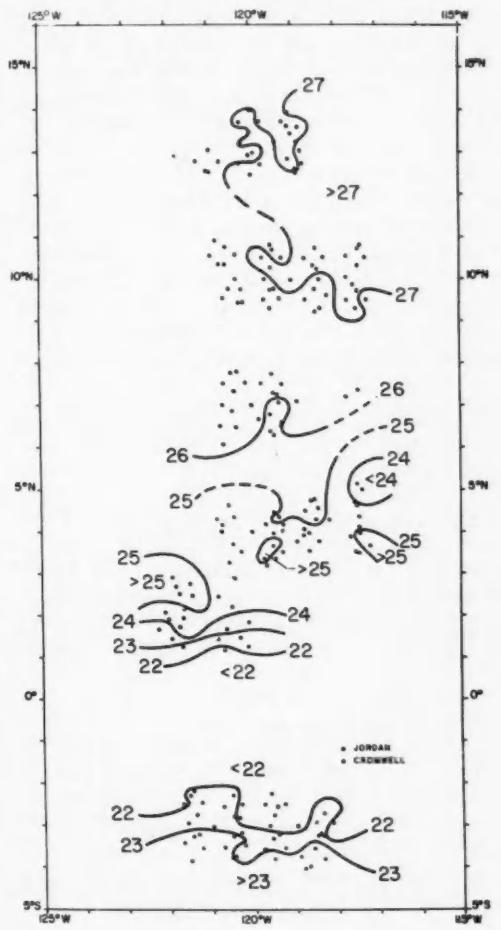


FIGURE 11.–Temperature (°C) section from lat. 15°N to 5°S along long. 119°W, cruise *Jordan* 60, 5-11 March 1971.



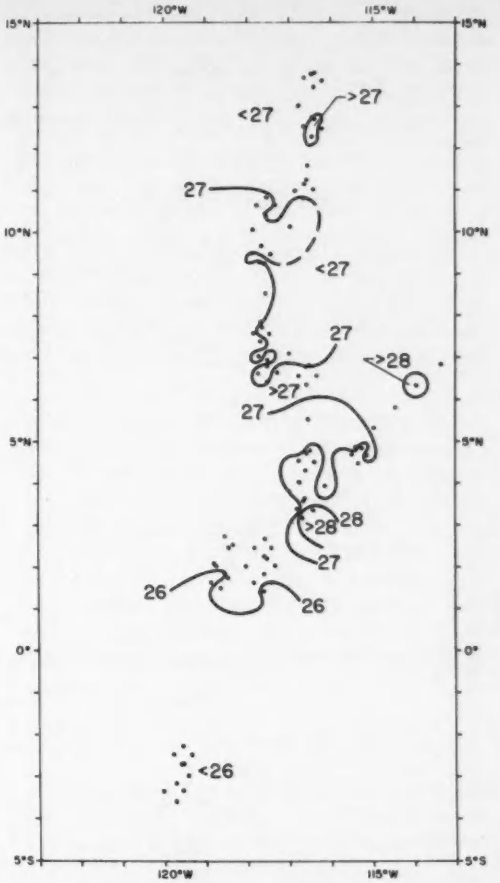


FIGURE 13.–Surface temperature (°C) during Part II operations, cruise *Jordan* 60, March-April 1971.

sections (Figures 10, 11). The temperature distributions were generally similar to those observed on the same meridian at the same time of year during EASTROPAC Expedition (M. Tsuchiya, pers. commun.). Surface temperatures suitable for skipjack, i.e., between 20° and 29°C, occurred at all latitudes on both cruises.

The distribution of surface isotherms (assumed synopticity) during Part II (fishing) operations on both cruises is shown in Figures 12 and 13. These figures have been compared, using overlays, with all charts of relative abundance of skipjack

FIGURE 12.–Surface temperature (°C) during Part II operations, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

(Figures 5, 6, 7, 8). The only apparent relationship between surface temperature and skipjack abundance appears to be the high abundance in the western part of the area of strong temperature gradient at lat. 1° to 3°N in November-December 1970.

Mixed Layer Depth

The depths (meters) of the bottom of the mixed layer are contoured at 20-m intervals in Figures 14 and 15 for Part II of the cruises. Figures 10 and 11 show the depths on Part I. Even though data are zonally discontinuous in parts of Figures 14 and 15, they are generally consistent with those of Cromwell (1958), Wyrtki (1964), and Love (1971b, 1972a, b, in prep.: EASTROPAC data).

In November-December 1970, the mixed layer depth was shallow (< 40 m) north of lat. 9°N, but south of there increased rapidly to > 100 m in the region of lat. 5°N. This ridge and trough are to be expected at the approximate northern and southern boundaries of the surface NECC. The gradient of change from this trough southwards to another ridge was particularly intense in the eastern edge of the area around lat. 4°N. In March-April 1971, the mixed layer was very shallow over most of the area surveyed south of lat. 10°N, becoming < 10 m in the region lat. 3° to 4°N. The even depth of the mixed layer from lat. 4° to 10°N

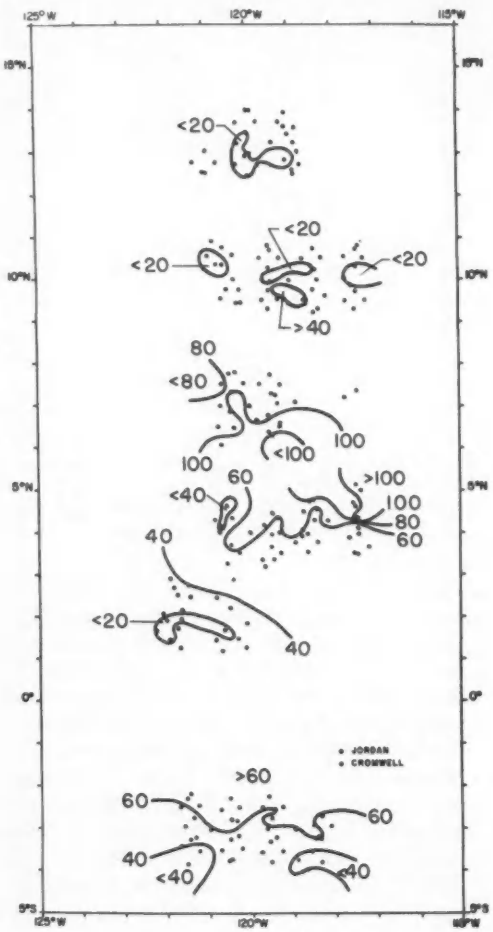


FIGURE 14.—Depth (m) of upper mixed layer, Part II operations, cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

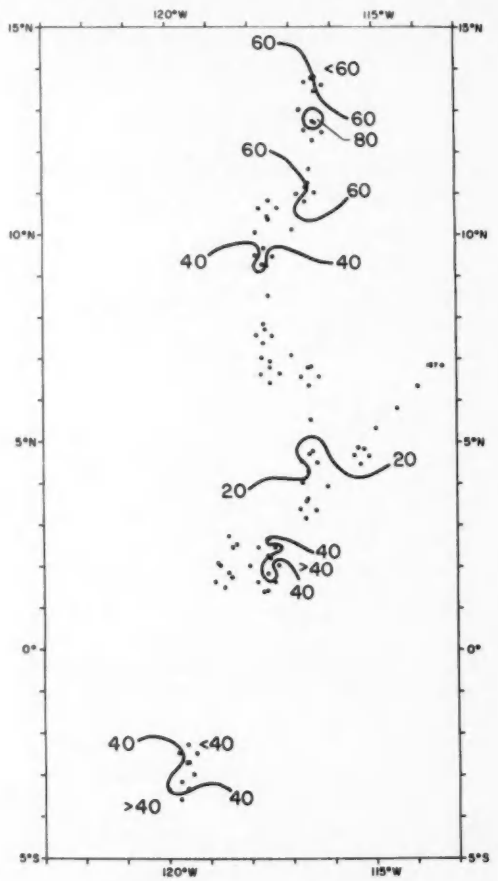


FIGURE 15.—Depth (m) of upper mixed layer, Part II operations, cruise *Jordan* 60, March-April 1971.

indicates the extreme weakness of the surface NECC at this time.

The charts of mixed layer depth have been compared by overlay with those of relative abundance of skipjack (Figures 5, 6, 7, 8). Areas of high relative abundance in November-December were generally close to ridges (< 40 m) in the mixed layer depth. There were exceptions, some of which are less obvious when utilizing schools/hour. There is no such trend in the March-April data.

Oxygen

Oxygen content (milliters/liter) was measured to 500 m, and sections showing oxygen distributions along the Part I transects of both cruises are presented in Figures 16 and 17. Sampling was also carried out in Part II fishing operations but for various reasons was more restricted than planned.

Figure 16 shows a strong oxycline (2 to 4 ml/liter) throughout the section of November 1971 parallel to the thermocline (Figure 10). In view of the probability of the lethal level of oxygen for skipjack being about 2.4 to 2.8 ml/liter (Anonymous 1973; R. Lasker pers. commun.), the depth of the 2.5-ml/liter isopleth may delimit the region of the water column suitable for skipjack. Its shallowest level in November-December 1970 (Figure 16) was about 50 m. In March-April 1971, (Figure 17) the oxycline was weaker and much reduced just north of the equator. The 2.5-ml/liter isopleth was on the average a little shallower than in November-December. The strong thermo-oxycline over most of the area on both cruises probably represented a bottom limit to vertical movement of skipjack, but even so at least the top 50 m of water were available to the fish.

The ridge in the oxycline at about lat. 10°N appears to be the western extension of the upper edge of the low oxygen-content water mass stretching out from the coast of Central America. (Tsuchiya 1968, Figure 7a, oxygen on the σ_T = 400 cl/T surface, which there is at < 100 m).

Currents

The positions of the boundaries between the North Equatorial Current (NEC), the surface North Equatorial Countercurrent (NECC), and the South Equatorial Current (SEC) have been indicated schematically in Figures 3 and 4. They were based on the slope of the thermocline during Part I and II operations. In November-December 1970 the surface NECC was confined to a narrow band between lat. 7° and 10°N, with a geostrophic flow of < 1 knot (44 cm/s). On the second cruise in March-April 1971 the surface NECC was located between lat. 4° and 8°N during Part I operations, but a short time later in Part II it had narrowed to between lat. 4°30′ and 7°N. The geostrophic flow was lower than on the previous cruise, < 0.5 knot (< 25 cm/s), except at the southern boundary, where the subsurface NECC may have surfaced and geostrophic flow was about 1.25 knots (65 cm/s). Average current charts for the area (Wyrtki 1965) show the surface NECC absent east of long. 120°W at this time of year. EASTROPAC data (Love 1971b, 1972a; M. Tsuchiya, pers. commun.) show the surface current absent at this meridian and time in 1967, but present in 1968.

Data from XBT records of the return passage of the *Cromwell* from the study area to Hawaii in November 1970 have been used to construct a diagonal temperature section from lat. 3°N, long. 124°20′W to lat. 16°30′N, long. 146°06′W (Figure 18). From the slope of the thermocline, the approximate boundaries of the surface NECC along the transect are defined as lat. 6° to 8°N (southern boundary) and lat. 10° to 11°N (northern boundary).

Chlorophyll

In November-December 1970, the range of surface chlorophyll *a* values was 0.03 to 0.22 mg/m^3, with a maximum (> 0.20) between lat. 0°30′ and 2°00′S. A small area with chlorophyll values > 0.20 also existed at about lat. 2°30′N, long. 119°W. An area of low chlorophyll (< 0.05) was located at lat. 9° to 10°N, long. 117° to 119°W. During March-April 1971, surface chlorophyll ranged from 0.03 to at least 0.25 and probably to about 0.40 mg/m^3. Maxima (> 0.20) occurred from lat. 9° to 11°N and lat. 13° to 14°N, and a minimum (< 0.05) occurred from lat. 5° to 7°30′N, all east of long. 118°W.

Zooplankton

All four sets of zooplankton data (1-m and 0.5-m nets, day and night) from Part II operations show broadly similar distributions for the same cruise on contour charts, and it is unnecessary to show them for both nets. The 0.5-m net catches probably give a better representation of the standing stock of small herbivores than the 1-m net catches, and

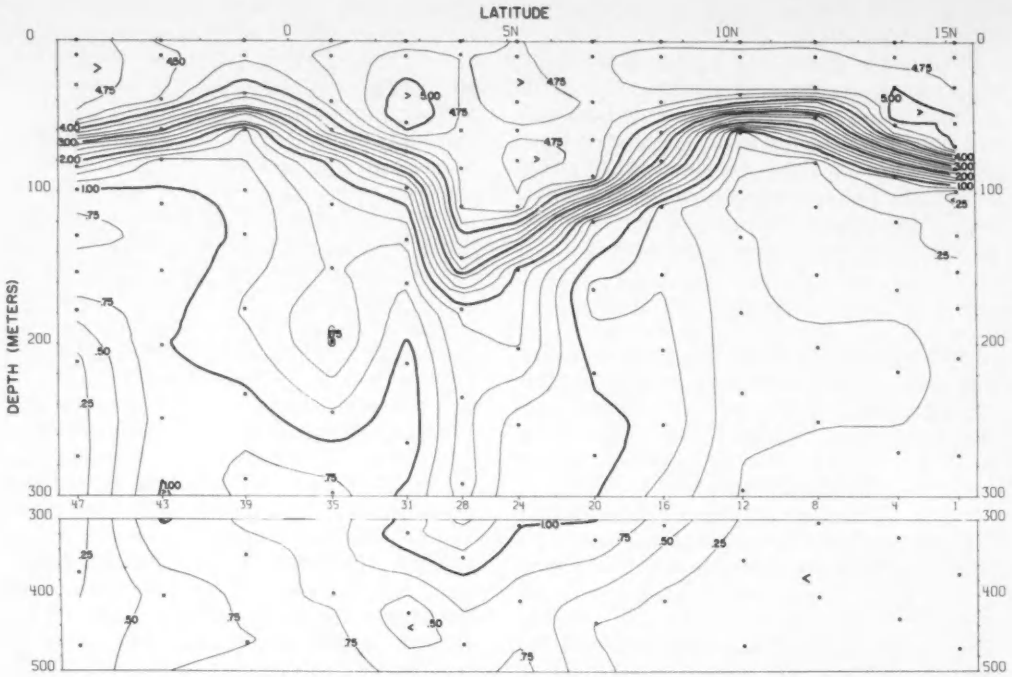


FIGURE 16.—Dissolved oxygen content (ml/liter), Part I transect, cruise *Cromwell* 51, 1-7 November 1970.

their distributions are charted here (Figures 19 to 22). Catches by the 1-m net are more likely to be related to skipjack tuna than those by the 0.5-m net, because more skipjack forage organisms occur in them. These relationships are investigated statistically in the next section.

The main features of the day and night zooplankton distributions in November-December 1970 are a maximum at about lat. 1° to 2°N, a minimum in the extreme north of the area, and a secondary minimum at about lat. 3° to 5°N. Maxima occurred in March-April 1971 at about lat. 3° to 6°N and 9° to 10°N; elsewhere at that period the catches were moderate with no conspicuous spatial minima except in the extreme north. Comparisons between Figures 19 to 22, and Figures 5 to 8, made by overlay, show no obvious relation between distributions of zooplankton and skipjack.

Skipjack Forage (and Zooplankton in Part)

One of the objectives of the cruises was to see if availability of offshore skipjack varied with the forage, as presumed by Blackburn (1965, 1969) and Blackburn and Laurs (1972); or with zooplankton, as suggested by Schaefer (1961); or with the arithmetic product of forage and zooplankton, as suggested by Riley (1963).

Charts of skipjack forage (in milliters/1,000 m^3), both day and night data, are shown in Figures 23 and 24 for both parts of the November-December 1970 cruise, and similarly in Figures 25 and 26 for the March-April 1971 cruise. Corresponding charts of total micronekton were very similar and are not given here. Data are available at Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif.

Measurements of day concentration of forage were more numerous than those of night concentration. Thus Figures 23 and 25 show more detail than Figures 24 and 26. Blackburn and Laurs (1972) showed that day and night distributions of forage were broadly similar in the area on a given cruise as far as locations of maxima and minima were concerned, although the night concentrations were about 10 times higher than day concentrations. Contours for day and night distributions were therefore drawn to agree with each other as

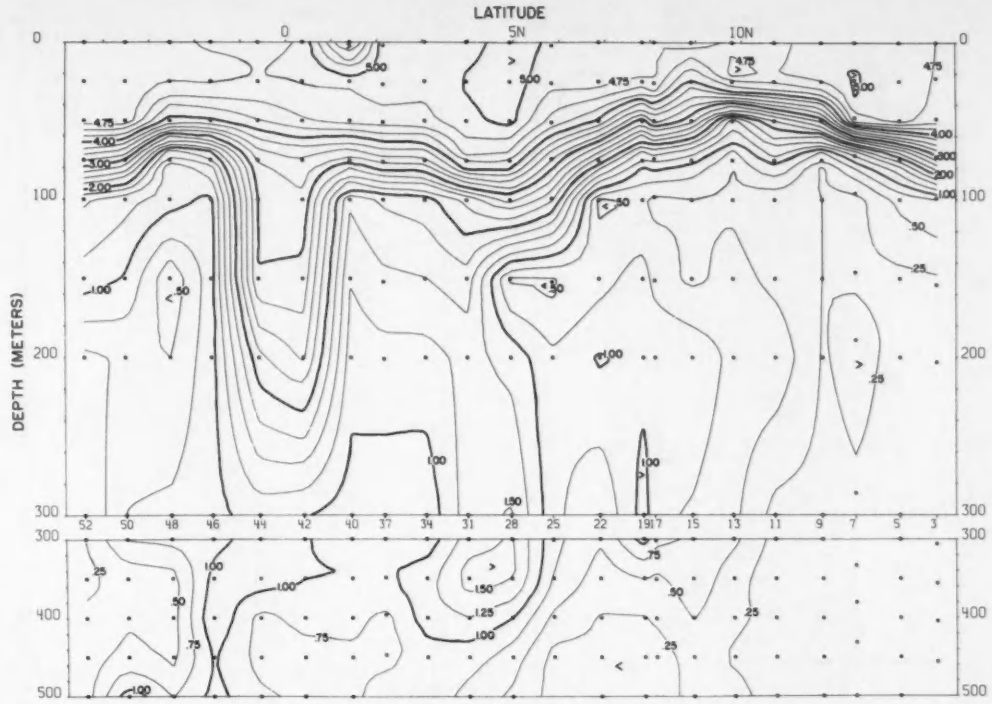


FIGURE 17.—Dissolved oxygen content (ml/liter), Part I transect, cruise *Jordan* 60, 5-11 March 1971.

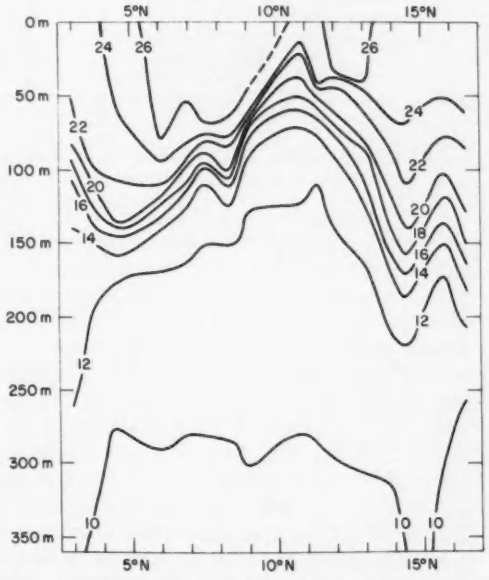


FIGURE 18.—Temperature (°C) section from lat. 3°N, long. 124°20′W, to lat. 16°30′N, long. 146°06′W, cruise *Cromwell* 51, November 21-26, 1970.

much as possible without violating the data. Fewer data were available for the March-April cruise than for the November-December one, for reasons given elsewhere.

According to Blackburn and Laurs (1972), the most conspicuous and consistent feature of day and night forage distributions in the study area is a zonally oriented maximum between lat. 0° and 5°N, which is probably associated with the equatorial upwelling as explained by King (1958). Figures 23 and 24 show this feature, and Figures 25 and 26 show one which is probably the same although it does not appear to be zonally oriented. Stations at the eastern end of the maximum in Figures 25 and 26 were occupied 13 days after the last stations at the western end were occupied, and the maximum could have moved north in the interval. Other maxima and minima in Figures 23 to 26 are smaller and less consistent in location between cruises.

The data from these micronekton net hauls, especially those for the March-April cruise which are very sparse, may not give a complete picture of the distribution of skipjack forage. On the March-

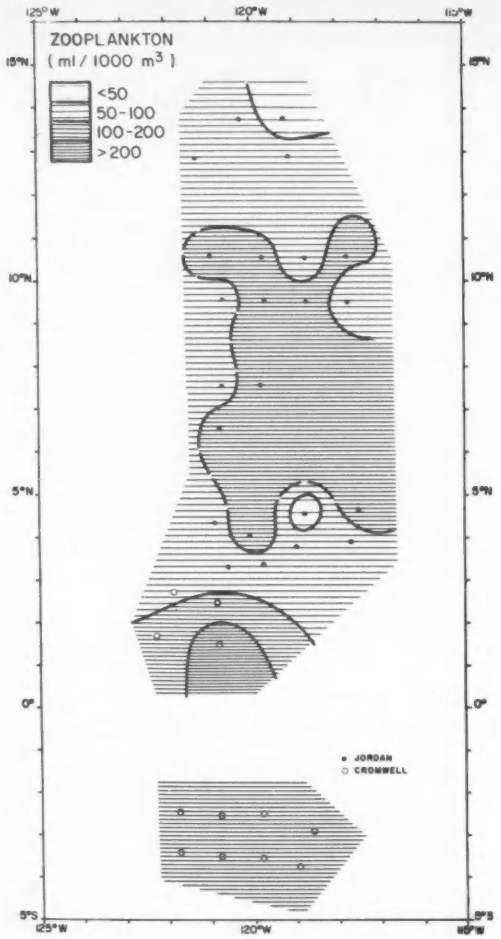


FIGURE 19.—Day standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

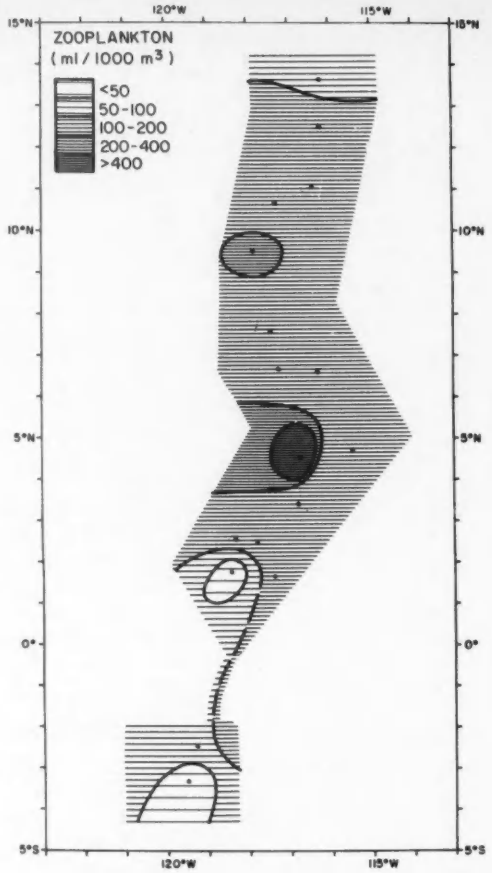


FIGURE 20.—Day standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruise *Jordan* 60, March-April 1971.

April cruise large catches of skipjack forage were obtained by midwater trawl as well as by micronekton net in the area of the maximum between lat. 0° and 5°N, and one was obtained also at about lat. 10°N where the micronekton net indicated a rather low concentration. This result from a single trawl haul thus indicates an area of rich forage of unknown extent at about lat. 10°N, which the sparse data from the micronekton net hauls do not show. The forage may have been patchy in this area.

The expected resemblance between the spatial distributions of forage and skipjack is not strongly evident when Figures 23 to 26 are compared with charts of skipjack availability on the same cruises (Figures 5 to 8). However, Table 3 shows that mean catch per line-hour and mean number of schools per hour for all fishing days in a zone of latitude was highest in November-December from lat. 1° to 5°N, where the principal forage maximum was located (Figures 23 and 24). Table 4 shows that the same indices were highest in March-April from lat. 9° to 11°N, where Figures 25 and 26 show no forage maximum, although one may have existed there as explained above. A secondary skipjack maximum occurred in March-April in the equatorial region, south of lat. 3°N, where a forage maximum was present.

Attempts were made to correlate forage con-

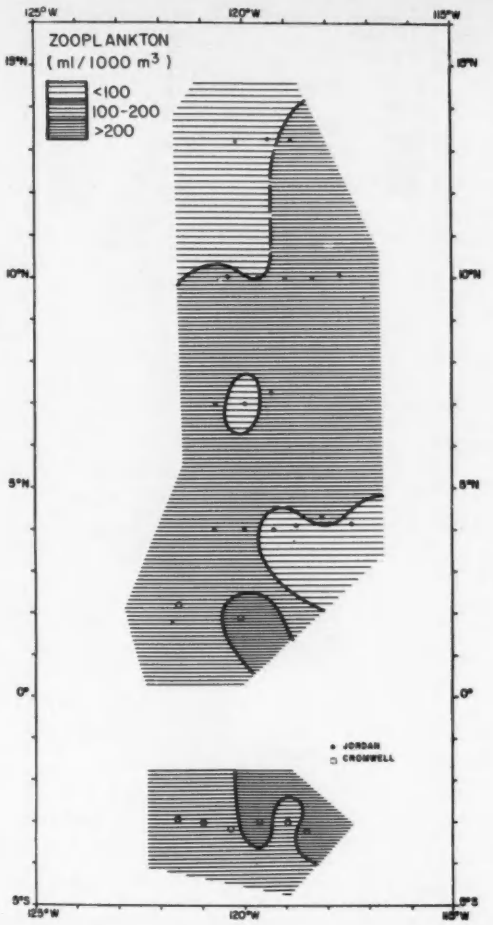


FIGURE 21.–Night standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

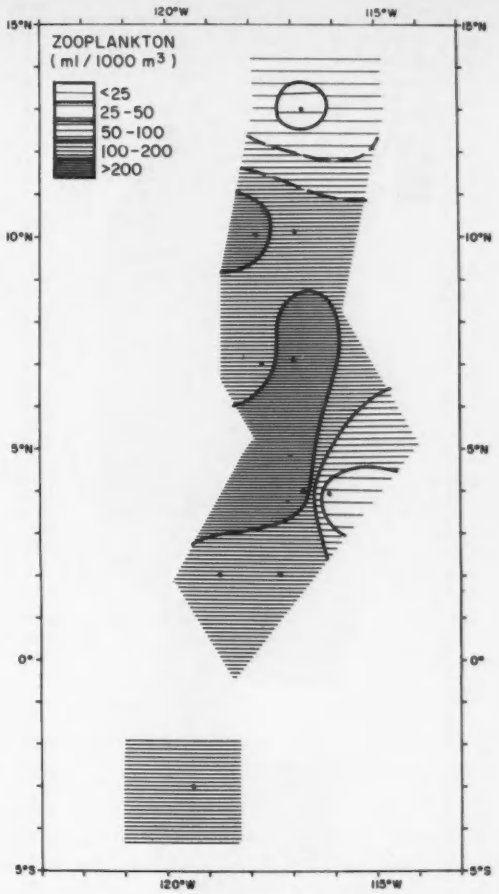


FIGURE 22.–Night standing stock of zooplankton by 0.5-m net (ml/1,000 m³), cruise *Jordan* 60, March-April 1971.

centration and related measurements with skipjack availability for all data from the study area. Table 11 gives the results of the tests using concentrations of day forage, day zooplankton, and their arithmetic product. Table 12 gives similar results using night concentrations. All variables were transformed to logarithms in order to bring distributions closer to normal, before correlation coefficients were calculated. A distinction is made between all skipjack and large skipjack; the latter excludes skipjack < 45 cm, which seem to be a separate age-group and exhibited some segregation from the other skipjack in space and time. Zooplankton data are from hauls of the 1-m net only, as explained above.

None of the 72 correlations in Table 11, involving day concentrations of forage and zooplankton with skipjack, are significant. On the other hand 4 of the 48 correlations in Table 12, involving night concentrations of forage and zooplankton with skipjack, are significant by the usual criteria and positive: two coefficients are above the 5% level of probability and two are above the 1% level. They refer only to availability of large November-December skipjack measured as catch per line-hour or schools per hour, in relation to night forage and to the product of night forage and night zooplankton, with both variables averaged over

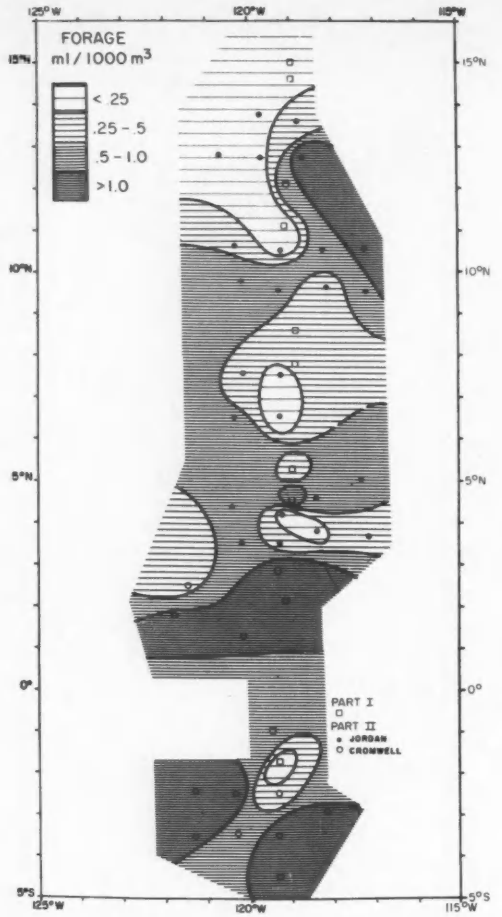


FIGURE 23.–Day standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

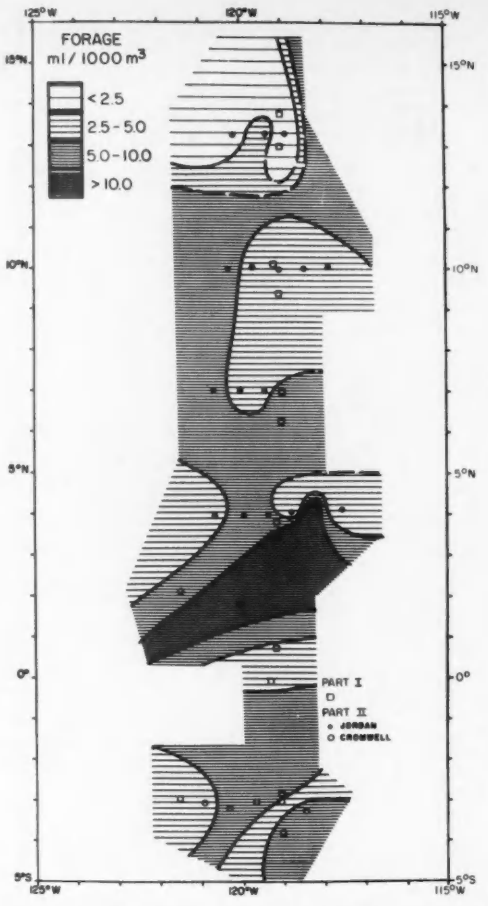


FIGURE 24.–Night standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruises *Jordan* 57-*Cromwell* 51, November-December 1970.

zones about 2° of latitude wide. There is no difference in the significance of coefficients depending on whether forage or forage × zooplankton was the variable, and no significant coefficients are obtained with zooplankton alone.

Table 13 gives the data that yielded the significant correlations between large skipjack and forage. The correlation coefficients are +0.947 with catch per line-hour and +0.886 with number of schools per hour, significant at the 0.5 and 2.0% probability levels respectively. The corresponding Spearman rank correlation coefficients are +0.952 and +0.905, both significant at the 5% level. No other grouping of 2°-latitude zones would have given so many zones with so much data in each (see Figure 3).

The significance of the four correlation coefficients in Table 12 has been disputed because of the much larger number of nonsignificant correlations in Tables 11 and 12 combined. It has also been pointed out that the two coefficients involving forage × zooplankton are not independent of the two coefficients involving forage alone. In our following comments we ignore all coefficients with forage × zooplankton, whether apparently significant or otherwise. We then have two possibly significant coefficients in a total of 80 for Tables 11 and 12, i.e., one in 40. From the previous paragraph, there is a chance of about one in 50 that

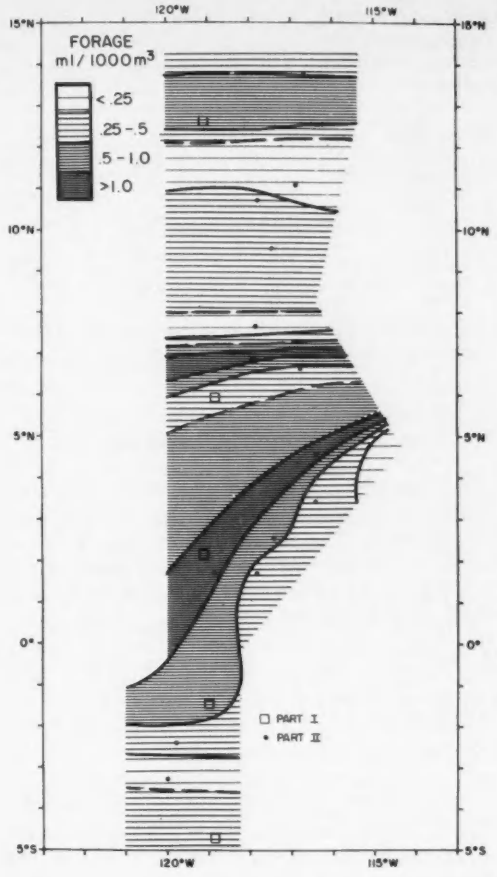


FIGURE 25.—Day standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruise *Jordan* 60, March-April 1971.

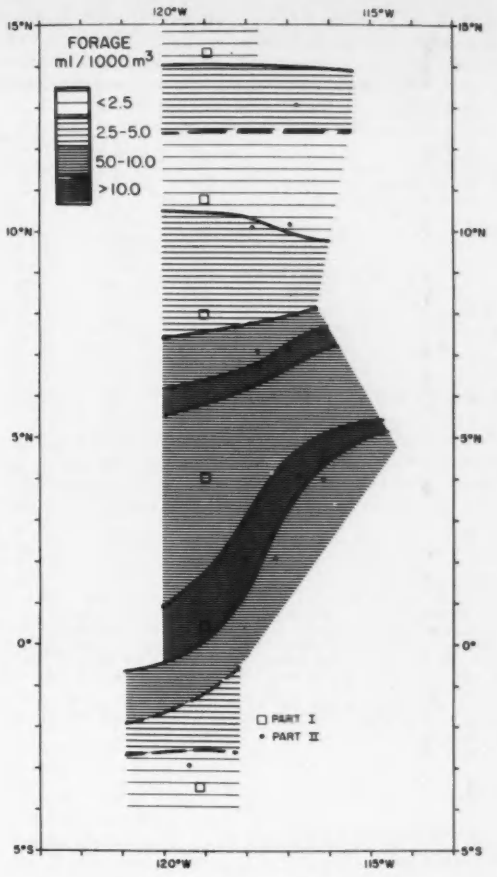


FIGURE 26.—Night standing stock of skipjack forage (ml/1,000 m³) (combined Part I and II data), cruise *Jordan* 60, March-April 1971.

the lower coefficient could have been so high with no correlation, and a corresponding chance of only about one in 200 for the higher coefficient. There seems no reason to presume nonsignificance, at least for the higher coefficient.

Significant correlations were not obtained for any data from the March-April cruise. Only two degrees of freedom are available to test the significance of correlations corresponding to the significant correlations in the November-December data. In any case the meager forage data for March-April seem not to have adequately depicted the actual conditions, as noted above. Relations of skipjack to forage are discussed later.

CRUISE 116 OF RV *CHARLES H. GILBERT*, OCTOBER-NOVEMBER 1969

In October-November 1969, the RV *Charles H. Gilbert* of the Honolulu Laboratory of the National Marine Fisheries Service made a cruise to collect samples of skipjack and other tunas for a subpopulation study. The main fishing operations were located in the same area as the combined cruise *Jordan* 57-*Cromwell* 51, though approximately 1 yr earlier. The fishing and environmental data are analyzed here in more detail than by Hida (1970). Figure 27 shows the cruise track of

TABLE 11.—Measures of daytime availability of skipjack correlated with day concentrations (ml/1,000 m³) of skipjack forage, zooplankton, and their arithmetic product. All tests were made with the variables transformed to logarithms. Numbers are pairs of observations from which correlation coefficients were calculated. No coefficients were significant. "All" means all skipjack; "large" means skipjack ≥45 cm.

Skipjack availability		Period	Data grouping[1]	Forage (F)	Zooplankton (Z)	F × Z
Catch/line-hour	All	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
	Large	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
Schools/hour	All	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6
	Large	Nov.-Dec.	A	35	33	33
			B	11	10	10
			C	6	6	6
		Mar.-Apr.	A	16	16	16
			B	4	4	4
			C	6	6	6

[1]A. Numbers to the right of this letter are numbers of 1° × 1° quadrants. For each quadrant skipjack availability is based on all observations for the day, and F and Z are each based on a single observation made in the quadrant during the day.

B. Numbers to the right of this letter are numbers of 1° zonal rows of quadrants with ≥2 quadrants per row. For each row skipjack availability, F and Z are means of the data for the individual quadrants.

C. Numbers to the right of this letter are numbers of 2° zonal rows of quadrants. For each row skipjack availability, F and Z are means of the data for the individual quadrants.

TABLE 12.—Measures of daytime availability of skipjack correlated with night concentrations (ml/1,000 m³) of skipjack forage, zooplankton, and their arithmetic product. All tests were made with the variables transformed to logarithms. Numbers are pairs of observations from which correlation coefficients were calculated. Significant correlations occurred as shown by * (5% level of probability) or ** (1% level) and were positive. "All" means all skipjack; "large" means skipjack ≥45 cm.

Skipjack availability		Period	Data grouping[1]	Forage (F)	Zooplankton (Z)	F × Z
Catch/line-hour	All	Nov.-Dec.	A	25	25	25
			B	6	6	6
		Mar.-Apr.	A	11	11	11
			B	4	4	4
	Large	Nov.-Dec.	A	25	25	25
			B	6**	6	6**
		Mar.-Apr.	A	11	11	11
			B	4	4	4
Schools/hour	All	Nov.-Dec.	A	25	25	25
			B	6	6	6
		Mar.-Apr.	A	11	11	11
			B	4	4	4
	Large	Nov.-Dec.	A	25	25	25
			B	6*	6	6*
		Mar.-Apr.	A	11	11	11
			B	4	4	4

[1]A. Numbers to the right of this letter are numbers of night stations, one station per night, at which observations of F and Z were made. F, Z, and F × Z for a night station were paired for correlation purposes with the mean of skipjack availability for the daytime periods immediately before and after the night on which the station was occupied, in closely adjacent 1° × 1° quadrants.

B. Numbers to the right of this letter are numbers of 2° zonal rows of quadrants and night stations. For each row skipjack availability is the mean of the data for the individual quadrants, and F and Z are the means of the data for the individual night stations.

TABLE 13.–Means of night skipjack forage and availability of large skipjack for 2° zonal rows of quadrants and night stations in November-December 1970, on which significant correlations in Table 12 are based.

Zone latitude	A Forage (ml/1,000 m³)	B Skipjack (catch/line-hour)	C Skipjack (schools/hour)
12°-14°N	1.54	0.020	0.060
9°-11°N	3.62	0.036	0.111
6°-8°N	3.98	0.044	0.070
3°-5°N	12.07	0.118	0.161
1°-3°N	10.23	0.189	0.235
2°-4°S	4.89	0.080	0.112

the *Gilbert* in relation to the area of the present investigations. Observations on tuna forage were not made.

Temperature and Surface Currents

Data from bathythermograph (BT) records have been used to make the two temperature sections shown in Figures 28 and 29. Surface temperatures everywhere were optimal for skipjack. The lowest temperatures on both sections occurred at lat. 0°30′S in the equatorial upwelling, namely < 24°C at long. 118°W and < 26°C at long. 137°W.

The approximate boundaries of the surface NECC during the cruise have been determined from the slope of the thermocline in Figures 28 and 29. On the outward track from Honolulu, the northern boundary of the NECC was lat. 10°N at long. 147°30′W, and the southern boundary, lat. 5°N at long. 142°15′W. On the south-north transect of the survey area, the southern boundary of the NECC was about lat. 6°N at about long. 120°45′W, and the northern boundary, lat. 9°N at about long. 129°30′W. The location of the surface NECC is shown in Figure 27.

Distribution and Relative Abundance of Troll-caught Tuna

Relative abundance of troll-caught tuna has been calculated as previously. The data are considered for: the area equivalent to the present study area plus the area fished by *Gilbert* south of lat. 5°S within long. 115°-125°W; the outward track from Honolulu to the area; and the inward track from the area to Honolulu. Total fishing effort in line-hours is given in Table 14.

The relative abundance of troll-caught skipjack and other tuna as catch/line-hour in the study area is shown in Table 15 by 1° latitudinal zones and

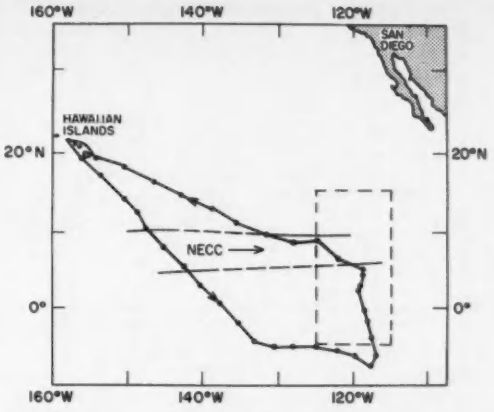


FIGURE 27.–Track of cruise *Charles H. Gilbert* 116, October-November 1969. Noon positions are indicated. Area of present investigations is outlined by dashed lines. NECC is surface North Equatorial Countercurrent.

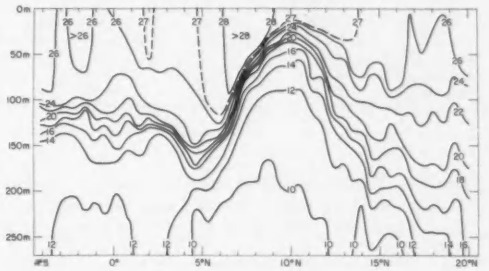


FIGURE 28.–Temperature (°C) section from lat. 19°55′N, long. 156°36′W to lat. 4°08′S, long. 133°40′W, cruise *Gilbert* 116, 3-13 October 1969.

surface currents. There was relatively little fishing effort (< 50 line-hours) in some latitudinal zones, which makes it difficult to define limits of maxima of skipjack abundance. However, the area from lat. 6° to 8°10′N is a maximum, with indices comparable with the highest ones in Table 3. Moderately high indices are seen at lat. 5° to 6°S and in the area lat. 0°-6°N, alternating with areas fished for less than 50 line-hours. Catch indices of other tunas were moderately high in the two zones where they occurred.

Relative abundance of skipjack as schools/hour in the area is given in Table 16 in two ways: firstly, as in previous sections of this report based on troll catches, and secondly, based on schools encountered during trolling and pole-and-line fishing. Usually, pole-and-line fishing was carried out subsequent to a jig strike, but occasionally not. The

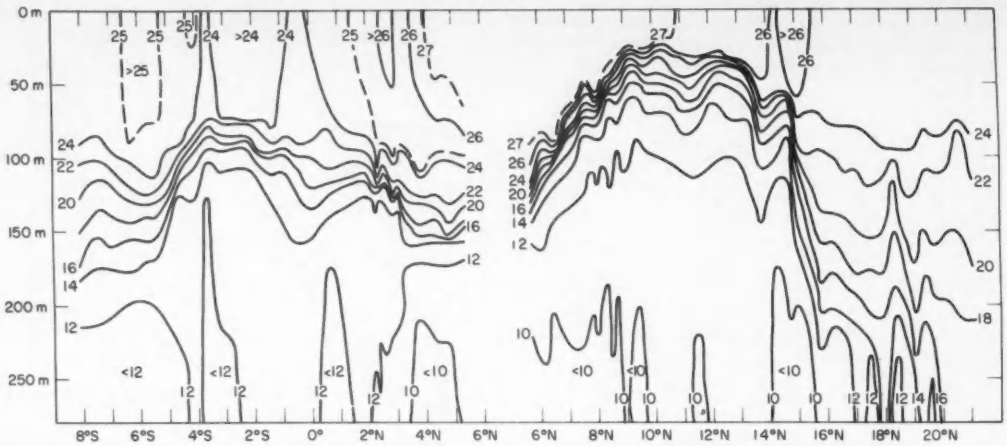


FIGURE 29.–Temperature (°C) sections from lat. 8°05′S to 5°21′N along long. 117° to 120°W, and from lat. 5°45′N, long. 120°14′W to lat. 21°03′N, long. 157°14′W, cruise *Gilbert* 116, 19 October-7 November 1969.

TABLE 14.–Total fishing effort Cruise *Gilbert* 116, October 1969.

Locality	Line-hours fished	
Study area		963
Outward track	382	788
Inward track	406	
Total		1,851

TABLE 15.–Relative abundance (catch/line-hour) of troll-caught skipjack and other tuna in the study area, Cruise *Gilbert* 116, October 1969. YF and BE mean yellowfin and bigeye. * means <50 line-h.

Zone latitude	Current system	Skipjack catch/ line-hour	Other tuna catch/line-hour
7°-8°10′N	NECC	0.240	0
6°-7°	NECC	0.342	0
5°-6°	SEC	0*	0
4°-5°	SEC	0.065	0
3°-4°	SEC	0*	0
2°-3°	SEC	0.087	0.138 (YF)
1°-2°	SEC	0*	0
0°-1°N	SEC	0.095	0
0°-1°S	SEC	0*	0
1°-2°	SEC	0*	0
2°-3°	SEC	0*	0
3°-4°	SEC	0*	0
4°-5°	SEC	0	0.093 (YF or BE)
5°-6°	SEC	0.097	0
6°-7°	SEC	0.017	0
7°-8°S	SEC	0.017	0

correlation between catch/line-hour and schools/hour was significant at the 1% level (r = 0.908, data of Tables 15 and 16), as on the cruises made in 1970 and 1971. The covariance analysis in Table 17 shows that the regressions of schools/hour on catch/line-hour for the three cruises did not differ significantly in slope, but differed in elevation.

TABLE 16.–Relative abundance (schools/hour) of skipjack in the study area, Cruise *Gilbert* 116, October 1969. *means < 9 h of observations

Zone latitude	Current system	Schools/hour	
		Based on troll catch	Based on total catch (troll plus pole-and-line)
7°-8°10′N	NECC	0.42	0.42
6°-7°	NECC	0.50	0.50
5°-6°	SEC	0*	0*
4°-5°	SEC	0.31	0.39
3°-4°	SEC	0*	0*
2°-3°	SEC	0.21	0.26
1°-2°	SEC	0*	0*
0°-1°N	SEC	0.34	0.34
0°-1°S	SEC	0*	0
1°-2°	SEC	0*	0*
2°-3°	SEC	0*	0*
3°-4°	SEC	0*	0*
4°-5°	SEC	0	0.22
5°-6°	SEC	0.15	0.15
6°-7°	SEC	0.05	0.05
7°-8°S	SEC	0.08	0.08

Table 16 shows the maximum at lat. 6° to 8°10′N, as in Table 15. Inclusion of the pole-and-line data increases the indices in other zones, i.e. lat. 4° to 5°N, 2° to 3°N, and 4° to 5°S. The range of the indices for schools/hour is about the same as for the other cruises.

Considerable catches of skipjack and other tuna were made on passage to and from the area. Data on relative abundance (catch/line-hour) are given in Table 18. Results should be used with care as fishing effort never exceeded 50 line-hours per day. There were moderate to high catch rates between lat. 4°45′ and 8°30′N (long. 148° to 138°W), with indices at about the same level as at lat. 6° to 8°10′N in the study area (Table 15). Catch indices for other tuna were low.

TABLE 17.–Analysis of covariance: schools/hour (Y) on catch/line-hour (X) for the 1969, 1970, and 1971 cruises, data of Tables 3, 4, 15, and 16.

Year	df	Σx^2	Σxy	Σy^2	b	df	Σd^2	M.S.
1969	7	0.0905	0.1144	0.1754	1.264	6	0.0308	0.0051
1970	11	0.0936	0.0904	0.1060	0.965	10	0.0187	0.0019
1971	11	0.0187	0.0402	0.1684	2.147	10	0.0822	0.0082
Within						26	0.1317	0.0051
Reg. Coef.						2	0.0223	0.0112
Common	29	0.2028	0.2450	0.4498		28	0.1540	0.0055
Adj. Means						2	0.0410	0.0205
Total	31	0.2286	0.2807	0.5394		30	0.1950	

F (slope) = 2.196, nonsignificant.
F (elevation) = 3.727, significant at 5%.

TABLE 18.–Relative abundance (catch/line-hour) of troll-caught skipjack and other tuna, on track to and from the study area, Cruise *Gilbert* 116, October-November 1969. YF and BE mean yellowfin and bigeye.

Date	Approximate position (start and finish of day's trolling) Latitude	Longitude	Current system	Fishing effort (line-hour)	Catch/line-hour Skipjack	Other tuna
Outward track:						
4 Oct.	16°15′ -17°30′N	153° -154°15′W	NEC	24	0	0
5	14° -15°15′N	150°30′-151°45′W	NEC	24	0.043	0.043 (YF)
6	12° -13°15′N	148°30′-149°30′W	NEC	23	0	0
7	9°30′ -10°45′N	147° -147°45′W	NEC/NECC	23	0.088	0
8	7°15′ - 8°30′N	144°30′-145°45′W	NECC	23	0.216	0
9	4°45′ - 6°15′N	142°15′-143°30′W	NECC/SEC	24	0.336	0
10	2°15′ - 3°30′N	139°45′-141°W	SEC	24	0.083	0.042 (YF)
11	1°15′N- 0°15′S	137°15′-138°15′W	SEC	24	0.083	0
12	1°30′ - 2°30′S	134°45′-136°W	SEC	24	0	0
13	3°45′ - 5°S	133° -133°45′W	SEC	48	0.042	0
14	5°S	130°15′-131°45′W	SEC	50	0.040	0
15	5°S	127°15′-128°45′W	SEC	48	0.063	0
Inward track:						
30 Oct.	8° - 9°N	127°15′-129°W	NECC	48	0	0
31	9° -10°N	130°45′-132°45′W	NEC	48	0	0
1 Nov.	10°45′ -11°45′N	134°30′-136°30′W	NEC	48	0.021	0
2	12°30′ -13°30′N	138°15′-140°15′W	NEC	48	0.042	0.063 (BE)
3	14°30′ -15°15′N	142° -144°W	NEC	48	0	0
4	16° -17°N	145°45′-147°45′W	NEC	48	0	0
5	17°30′ -18°30′N	149°30′-151°30′W	NEC	48	0	0

Pole-and-Line Fishing

Hida (1970) recorded 109 schools of fish sighted during cruise *Gilbert* 116: 27 skipjack, 1 bigeye tuna, 1 yellowfin tuna, 2 mixed tunas (skipjack-bigeye-yellowfin), 13 of nontuna species, and 65 unidentified. On the outward track and in the southern part of the study area (from lat. 4°27′S, long. 133°22′W, to lat. 6°25′S, long. 117°47′W: 13 to 20 October 1969), at least 13 tuna schools were sighted or discovered by jig strikes. They were chummed, but did not respond to live bait. From 21 to 27 October in the study area (between lat. 4°09′S, long. 117°47′W and lat. 5°04′N, long. 118°50′W), at least 11 schools of tuna were chummed with live bait and of these 6 were successfully fished by pole-and-line (these schools were sighted and pursued, not discovered by jig strikes). Details are given in Table 19. All schools fished successfully by pole-and-line were located in the South Equatorial Current. These results are of special interest because they were obtained by a commercial fishing method. Trolling is not a commercial fishing method for skipjack in U.S. fisheries.

Size of Skipjack and Other Tuna

Table 20 shows the percent of skipjack in three broad size categories by fishing method and area. Only one skipjack (45 cm) was taken on the inward track to Honolulu. In the study area the percentages in size groups are similar for the two fishing methods. The percentage of fish < 45 cm, namely 8 to 11%, is much the same as that in the area in November-December 1970. The smallest skipjack measured 34 cm. The largest skipjack (mean lengths > 75 cm) were taken in the extreme south of the area. Elsewhere mean sizes of skipjack ranged from 46 to 67 cm, with two exceptions: 34 cm (trolling) and 40 cm (pole-and-line). On the outward track to the area, troll-caught skipjack

TABLE 19.—Details of successful live-bait pole-and-line fishing of tuna schools in the study area, Cruise *Gilbert* 116, October 1969. SJ, YF, and BE mean skipjack, yellowfin, and bigeye.

Date	School data[1]	No. birds	Approximate position Lat.	Long.	Time successful fishing commenced	Species	No. taken	Size (cm) Range	Mean	No. measured	Approximate weight (lb) Range	(Mean)
Oct.												
21	—	15 birds	4°S,	118°W	0710[2]	SJ	13	37-52	40	13	—	(3)
						YF	8	37-43	39	8	—	(3)
						BE	7	37-43	41	7	—	(3)
24	—	Flock, 50	2°N,	119°W	1220[3]	SJ	213	64-70	68	50	15-18	(17)
26	Breezer	Flock, 150	4°N,	119°W	1125[4]	SJ	519	41-56	47	60	3-8	(5)
						YF	28	40-58	47	28	4-8	(4)
						BE	13	41-46	43	13	3-4	(4)
	Boiler	Flock, 500	4°N,	119°W	1707[3]	BE	97	50-81	69	33	10-20	(—)
27	Boiler	Flock, 300	4°50′N,	118°25′W	0650[2,3]	SJ	49	47-67	59	49	—	(10)
	Breezer	Flock, 250	5°N,	118°49′W	1031[3]	SJ	110	48-61	52	54	—	(—)

[1] After Scott (1969).
[2] Poor biting school.
[3] School abandoned when sample complete.
[4] Very large school still around ship at 1500 h.

TABLE 20.—Skipjack by size categories as percent of total, and by fishing method and area, Cruise *Gilbert* 116, October 1969.

Size (cm)	Study area Troll	Pole-and-line	Outward track to study area Troll
<45	8.0	11.2	80.0
45-59.9	52.0	57.0	15.0
≥60	40.0	31.8	5.0
Total skipjack	25	223	20

ranged from 29 to 78 cm, mean 41 cm. Although very few were caught, the high percentage of fish < 45 cm is of interest.

In the study area all small fish (< 45 cm) were from areas of the South Equatorial Current. In the area west of long. 125°W, small fish were found in all three current systems (NEC, NECC and SEC), approximately from lat. 15°15′N, long. 151°45′W to lat. 0°25′S, long. 137°15′W.

Skipjack percent length frequency distribution by 2-cm classes is given in Figure 30 for the study area in October 1969. There appear to be three

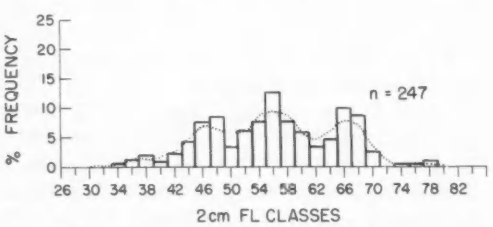


FIGURE 30.—Skipjack percent length frequency distribution (study area only), cruise *Gilbert* 116, October 1969. Smoothed curves are from 3-figure moving average. Stated length indicates midpoint of class.

modes at 46, 56, and 66 cm. Inclusion of data from the outward track would increase the probability of another mode at 36 to 38 cm. The November-December 1970 length data for the study area were similar and showed modes at 36, 48, and 58 cm; only the 66-cm mode was absent (Figure 9). The similarity suggests that the modes of 1969 (October-November) and 1970 (November-December) represent age-classes.

On the outward track yellowfin were small, mean lengths 37 and 32 cm, and on the return track bigeye had a mean length of 57 cm (Table 18). In the study area mean lengths of yellowfin ranged from 39 to 47 cm and those of bigeye from 41 to 69 cm (Table 19).

Sex and Maturity of Skipjack and Other Tuna

The sex ratio of skipjack in the study area was males to females 1:0.89 (n = 249), and on the outward track 1:1 (n = 20).

Tuna gonads taken on cruise *Gilbert* 116 were recorded as immature, maturing, mature, or spent and can be roughly compared with those for the other two cruises. The number of skipjack gonads in each maturity stage by size of fish is given in Tables 21 and 22 for the study area and outward track.

Apart from three females, all immature fish (19% of total in the study area and 80% of total on outward track) were < 50 cm. The principal difference between fish caught on this cruise and the other two is the virtual absence of spent fish. Most fish (> 74%) were classed as maturing, and

this could indicate that they were southern spawners. All troll-caught yellowfin tuna were immature, sex indeterminate, as were the bigeye except for one immature male of 59 cm.

DISCUSSION AND CONCLUSIONS

Gulland (1971) reviewed research findings which indicate that skipjack is the most abundant tuna in the Pacific, except possibly for frigate mackerel which is a small and presently valueless species. Our results and those of Hida (1970) show that each of the three cruises yielded many more skipjack than all other species of fish combined, including nontunas and unidentified fish (Tables 2, 15, 18, 19). On each cruise some skipjack were obtained in almost every part of the area in which fishing was done. Occurrences of other tunas (yellowfin, bigeye, and frigate mackerel) were much fewer and more localized (Tables 2, 3, 4, 15, 18, 19).

Our results also support the general hypothesis of Rothschild (1965), Williams (1972), and others that skipjack migrate as juveniles from central Pacific spawning areas towards the American coast, spend part of their adolescent life near the coast, and then return to the central Pacific. The present study area lies between the spawning areas and the coast. Thus one would expect the skipjack in that area to include, at times, individuals both smaller and larger than those typical of coastal waters. We have demonstrated their occurrence (Tables 6, 7, 20; Figures 9, 30).

Matsumoto (1966), Ueyanagi (1969), and Love (1970, 1971a, in prep.: EASTROPAC data) indicate that skipjack larvae are rare east of long. 130°W in the tropical Pacific, but increase rapidly west of that meridian. Thus our study area is close to a spawning region. One would then expect some of the large skipjack in the study area to have maturing, spent, or spent-recovering gonads at times, and this condition was found (Tables 8, 9, 10, 21, 22). The occurrence of spent-recovering and resting gonads in November-December suggest principally northern summer spawning, especially since no spawned-out fish were taken south of lat. 3°N. The presence of spent-recovering fish in March-April perhaps indicates southern summer spawners (northern winter); however, the occurrence of skipjack with maturing gonads at this time may also signify northern summer spawners. Fish taken on the two cruises may be of two spawning groups, northern and southern (see Williams 1972).

The juvenile skipjack (< 45 cm) constituted a small proportion, 13% or less on each cruise, of the total skipjack caught in the study area. Their distribution varied spatially and temporally (Tables 6, 7, 20; text p. 389). On the cruise of October-November 1969 they were found only in the South Equatorial Current, but the North Equatorial Current was not sampled. In November-December 1970 they were found principally in the North Equatorial Current and sparsely in the South Equatorial Current. In March-April 1971 they were very scarce or absent in all parts of the study area. West of long. 125°W in October-November 1969, some juveniles were taken in the North Equatorial Countercurrent as well as in the other two currents. It does not seem possible from these data to make a choice among any of the three models of coastward migration of juveniles proposed by Williams (1972), or to eliminate any of them from consideration. Data from other periods of the year are desirable.

From previous studies by Williams (1970), adult skipjack (> 45 cm) were expected to occur in waters of surface temperature 20° to 29°C, but not preferentially at particular temperatures within that range. All waters of the study area had such temperatures on all cruises (Figures 10, 11, 12, 13, 28, 29). Thus they were all suitable for skipjack as far as temperature was concerned, and skipjack occurred to some extent in most of them (Figures

TABLE 21.—Number of skipjack gonads in each maturity stage by size of fish, study area, Cruise *Gilbert* 116, October-November 1969.

Size class (cm)	Immature		Maturing		Mature	
	M	F	M	F	M	F
30-39.9	2	6	1			
40-49.9	16	21	21	4		
50-59.9		3	48	38	3	6
60-69.9			38	34	1	2
70-79.9				1	2	2

Totals: males (M) 132, females (F) 117.

TABLE 22.—Number of skipjack gonads in each maturity stage by size of fish, outward track, Cruise *Gilbert* 116, October 1969.

Size class (cm)	Immature		Maturing		Mature		Spent	
	M	F	M	F	M	F	M	F
20-29.9	2							
30-39.9	3	4						
40-49.9	4	3						
50-59.9			1			1		1
60-69.9								
70-79.9						1		

Totals: males (M) 10; females (F) 10.

5, 6, 7, 8; Tables 15, 16, 19). No relation appears between skipjack distribution and particular temperatures within the 20° to 29°C range.

Blackburn and Laurs (1972) expected adult skipjack to be distributed like their forage in offshore areas where all surface temperatures are suitable. This was because Blackburn (1969) found such a relation for skipjack in waters of suitable temperature near the coast, and Magnuson (1969) found that skipjack eat the equivalent of 15% of their body weight per day when fed to saturation. Thus adult skipjack would probably be most numerous in the latitudinally oriented zones of abundant forage which occur offshore, with forage concentrations comparable to those in coastal waters, during their westward movement from the coast to the spawning areas (Blackburn and Laurs 1972). They would probably migrate slowly through forage-rich zones or areas and quickly through those poor in forage, and thus be more abundant per unit area in the forage-rich situations.

Blackburn and Laurs (1972) showed from EASTROPAC data that the richest and most persistent zones of skipjack forage in our study area occurred a few degrees north and sometimes south of the equatorial upwelling. They also recognized a less conspicuous zonal forage maximum near the northern boundary of the North Equatorial Countercurrent, probably associated with high biological production over the shoal pycnocline. Data from the November-December cruise show the expected maxima of forage and skipjack near the Equator, but do not clearly show a maximum of either on the north side of the Countercurrent (Figures 23, 24; Table 3). Tables 12 and 13 show two statistically significant positive correlations between availability of large skipjack and their forage on the same cruise, although only for night concentrations of forage and for data averaged over a 2° zone of latitude. As mentioned earlier the actual significance may be disputable for the lower of these correlation coefficients, but not for the higher one, taking the total number of correlations in Tables 11 and 12 into account. Correlations between skipjack and day forage were not significant (Table 11).

Skipjack probably do much of their feeding in the daytime (Nakamura 1962) although forage is much scarcer in the upper water layers by day than by night. Thus the lack of relation between skipjack and day forage may seem surprising. One could however interpret these results as follows. Spatial distributions of day and night forage broadly coincide (Blackburn and Laurs 1972) because they are determined by the same physicochemical and basic biological features of the environment. Skipjack tend to occur in broad zones where both kinds of forage are initially abundant, for reasons suggested above. Within these zones they aggregate in the richer patches of day forage and eat them down, whereby their relation with the day forage will be sometimes direct and sometimes inverse. If they eat the much more abundant night forage they probably do not so frequently reduce it to a point at which the relation becomes inverse.

The significant November-December correlations become nonsignificant when data for skipjack < 45 cm are included (Table 12). Thus juvenile skipjack may be distributed in relation to a different kind of forage, or possibly to other environmental properties excluding forage. Blackburn and Laurs (1972) made no statement about ecology of juveniles.

The relatively sparse data for the March-April cruise of 1971 show a forage maximum near the Equator but not clearly elsewhere (Figures 25 and 26), although one may nevertheless have been present near the northern edge of the Countercurrent, as mentioned previously. The principal maximum of skipjack in March-April 1971 was located slightly north of the North Equatorial Countercurrent, and there was a secondary maximum near the Equator (Table 4). Data on skipjack and forage yielded no significant correlations. They were probably too sparse to do so (Table 12).

Tables 3 and 4 show that skipjack were less abundant in the North Equatorial Countercurrent than in either of the adjacent currents, on both the 1970 and 1971 cruises. This was expected because neither Blackburn and Laurs (1972) nor we found much forage in the Countercurrent. However skipjack availability was much higher in the Countercurrent (lat. 6° to 8°N) than in the South Equatorial Current on the 1969 cruise (Tables 15, 16). Forage data are lacking for the cruise, but it is not likely that forage was highly abundant in the North Equatorial Countercurrent. We note that the large skipjack taken in October-November 1969 had sexually maturing or mature gonads (Table 21), whereas most of those taken on the other cruises had spent, spent-recovering, or resting gonads (Tables 8, 9). Possibly the October-November fish were close to spawning, and thus

becoming distributed in accordance with the requirements of their larvae. There is evidence that skipjack larvae occur only at sea temperatures from 23° to 31°C and are most common at about 29° to 30°C (Inter-American Tropical Tuna Commission 1971). Maximum surface temperatures in the study area in October-November 1969 were between 27° and 28°C and occurred from about lat. 4° to 11°N (Figure 29). Thus the Countercurrent waters at lat. 6° to 8°N could have been particularly suitable for the survival of skipjack larvae, and the parent fish may have been becoming distributed accordingly.

We found no direct relations between skipjack and mixed layer depth, dissolved oxygen, surface currents, chlorophyll, or zooplankton although some of these properties and features should have indirect effects on skipjack through their effects on temperature and forage. Some of them could also have direct effects upon larval or juvenile skipjack. Significant correlations between skipjack and zooplankton were not found (Tables 11, 12). Significant correlations between large skipjack and forage are also significant between skipjack and the arithmetic product of forage and zooplankton, but not between skipjack and zooplankton alone.

Although this paper has contributed to our knowledge of the distribution and relative abundance of skipjack in the offshore eastern tropical Pacific, where little information was previously available, the prospects for commercial fishing remain unknown. Our simple experimental fishing procedures served to identify zones of maximum occurrence of skipjack, but commercial trials will be needed to show if those zones can be exploited profitably. Ideally there should be trials by live-bait boats as well as purse seiners, in view of the fact that live-bait fishing gave good results on an experimental scale during the 1969 cruise. Our data and interpretations should be useful as a guide to those who make these tests.

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REPRODUCTION AND RECRUITMENT OF THE BRACKISH WATER CLAM *RANGIA CUNEATA* IN THE JAMES RIVER, VIRGINIA[1,2]

THOMAS D. CAIN[3]

ABSTRACT

Reproduction and recruitment of the brackish water clam *Rangia cuneata* were investigated in the James River, Va., from February 1970 to January 1972. Histological examinations of gonads were made, newly set clams were collected, and temperature and salinity measurements were taken from three populations living in different salinity regimes.

Gametogenesis began in April and ripe gonads were found from May to late November with no inactive period. From observations of set abundance, two periods of spawning were determined: one in early through midsummer, coinciding with the beginning of spawning as determined from gonadal examinations; and a second and longer period in late fall and early winter, with an increased percentage of partially spawned and spent clams. Gametogenesis ceased in December through March as residual gametes were cytolyzed. Sex was not detected during this last phase. More females than males were found in the upstream (lower salinity) populations. Temperature was important in initiating gametogenesis in the spring and midsummer. Spawning correlated best with changes in salinity to approximately 5 °/₀₀.

Over its estuarine range, salinity has a controlling effect on *Rangia* spawning and recruitment. Seasonal reduction in input of freshwater (increased seawater intrusion) is needed to induce spawning and recruitment in upstream populations. Best recruitment occurred to the middle of the habitat range which has an annual salinity change from fresh to 5°/₀₀.

A southern species of clam, *Rangia cuneata* (Gray) has in the last 15 yr extended its range into Chesapeake Bay estuaries (Hopkins and Andrews 1970). This clam occupies an otherwise "open niche" in the oligohaline region of these estuaries. Although species diversity is usually low, there may be large numbers of individuals of species adapted to this environment. In the upper James River estuary, *Rangia* accounts for nearly 95% of the benthic biomass.

Rangia is important both ecologically and commercially (Hopkins 1970). It provides a substantial food source for several species of fish and crabs (Darnell 1958), and waterfowl (Wass and Wright 1969). It is ecologically significant because it converts detritus into biomass that can be utilized by these organisms (Odum and Copeland 1969).

Not only is *R. cuneata* a species for which low salinity, 1-15°/₀₀, is optimal; it is also a species which evidently cannot maintain a population outside this range (Hopkins 1970). That *Rangia* thrives in a zone unfavorable for most animals indicates it has some unusual adaptations. Despite its abundance in favorable environments and long history on the Gulf Coast, this clam has received little attention.

The study reported here concerns the reproductive cycle and recruitment of *Rangia cuneata* in the James River. The major objectives were to: (a) study the gametogenic cycle of *Rangia* from histological sections; (b) determine differences in gametogenesis or spawning of clams over the species range in the estuary; (c) investigate, from analysis of field data, the influence of temperature and salinity on initiation of gametogenesis and spawning; (d) corroborate gametogenic findings by collecting newly set clams; and (e) determine the duration of the larval period and differences in set abundance in the estuary.

Fairbanks (1963) studied the spawning cycle of *Rangia* in Lake Pontchartrain, La., but it is known that physiologically different races of bivalves can occur at different latitudes (Loosanoff 1969). Cain

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(1973, 1974) reported on the laboratory spawning of *Rangia* and the combined effects of salinity and temperature on embryos and larvae.

The impending action (at the time the work was initiated) of discharge of waste heat into the *Rangia* community by the Virginia Electric and Power Company's (VEPCO) Nuclear Generating Station at Surry, Va., was a further impetus to the study of the reproductive cycle, especially those factors that initiate gametogenesis and spawning.

DESCRIPTIONS OF THE STUDY AREA

The study area in the James River is a transition region between freshwater and salt water. The area has a seasonably variable salinity that ranges between about 0 and 15‰, depending on the volume of freshwater input. In the spring, high river flow covers most of this region (except station A) with freshwater (Figure 1). Occasionally, in late summer and fall the study area may exhibit measurable salinity as far upstream as station C. The mean annual discharge of the James River is approximately 212 m^3/s (7,500 cfs).

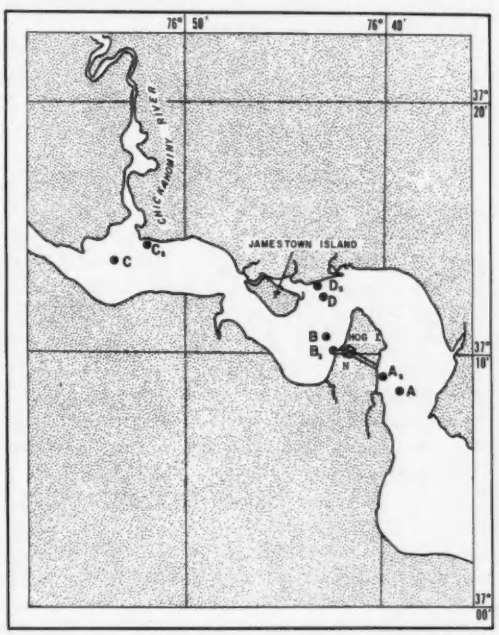

FIGURE 1.–Location of sampling stations for *Rangia cuneata* in the James River, Va. (N = nuclear generating station).

Field and hydraulic model studies of the James River estuary have shown a two-layer density flow pattern, in which the deep, more saline water has a net upstream flow and the surface, fresher water has a net downstream flow. The net sediment transport of the two-layer section averaged over many tidal cycles is upstream (Pritchard 1952). The transition section of the James River is characterized by high natural turbidity and sedimentation from the flocculation of river-borne sediments.

The distribution of bottom sediment types in the James River estuary has been studied by Nichols (1972). His survey indicates silt-clay substrates at stations A, B, C, and D and sand substrates at locations As, Bs, Cs, and Ds.

The distribution of *Rangia* in the James River was found to be approximately from nautical mile 25 to 55 above the river mouth (Figure 2). The downriver extent of its range overlaps the habitat of typical estuarine organisms such as the oyster; at the upriver limit *Rangia* is associated with completely freshwater forms such as freshwater mussels. In the oligohaline portion of its range it is typically associated with the polychaetes *Scolecolepides viridis* and *Laeonereis culveri;* the crustaceans *Cyathura polita, Corophium lacustre,* and *Gammarus* sp.; and the bivalves *Macoma balthica, Brachidontes recurvus,* and *Congeria leucophaeta.*

METHODS AND MATERIALS

The reproductive cycle was investigated by collecting clams at stations A, B, and C (Figure 1). Station A was near the downstream range of the clam. Station B was 18.5 km above station A. Station C was located (18.5 km above station B) near the mouth of the Chickahominy River in order to include part of the clam's range which seldom experiences salinity changes. All stations were located at approximately the same depth (3-4 m). The clams used in this study were collected from a predominantly silt-clay substrate. Although Tenore et al. (1968) indicated that such sediments were detrimental to *Rangia*, the clams at the various stations appeared to be thriving over the 2-yr study.

Beginning in February 1970 approximately 20 clams, 30-40 mm long, were collected at stations A and B using a modified oyster dredge. Attempts were made to collect clams at these stations every

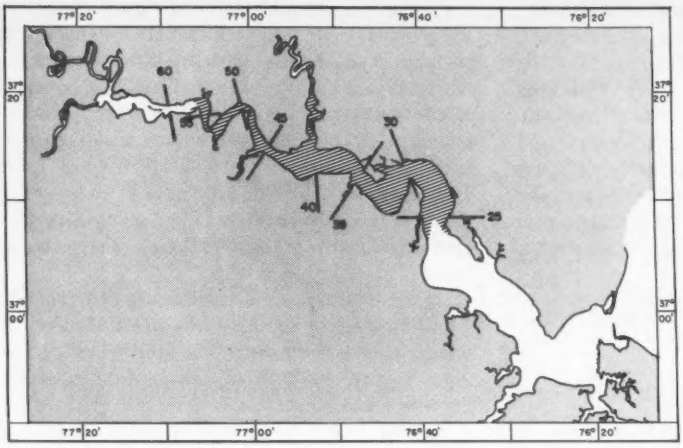

FIGURE 2.—The distribution of *Rangia cuneata* in the James River, Va. Segments are at 5-nautical mile intervals.

2 wk, but bad weather and boat failures occasionally delayed this to 3 wk. Beginning 22 September 1970 collections at station C commenced. Collections at all stations were terminated in January 1972.

In the laboratory these clams were measured, weighed, shucked, and the gonads dissected out and placed in a solution of alcohol, Formalin,[4] and acetic acid (AFA) for fixation. Gonad tissues were sectioned at 7-10 μm with a rotary microtome, stained with Delafield's hematoxylin, and counterstained with eosin. Gonad tissue stage of development was determined following the scheme of Ropes (1968) who categorized the seasonal gametogenic cycle of *Spisula solidissima* as: early active, late active, mature, partially spawned, or spent. Similar stages of development were first described by Ropes and Stickney (1965) for *Mya arenaria* and have subsequently been used for two other members of the family Mactridae; *Mulinia lateralis* (Calabrese 1970), and *Tresus capax* (Machell and De Martini 1971). The number of clams in each category, regardless of their sex, was recorded for each sample.

The sex ratio of clams from each station was calculated and a chi-square test used to establish goodness of fit to a 1:1 ratio.

During June 1970, clams collected at stations A and B were placed in four groups (5-10, 11-20, 21-30, and 41-50 mm). These clams were sectioned and stained to determine the size at which they contain reproductive products.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Set Collectors

Collectors used to determine the time and intensity of setting were placed at stations A, B, C, and D and inshore from these areas in shallow, sandy areas (Figure 1). These stations were designated as As, Bs, Cs, and Ds. Stations A, As, B, Bs, and Ds were examined from June 1970 and C, Cs, and D from September 1970, at approximately 2-wk intervals until January 1972.

The set collector was a plastic gallon jar with an 8.7 cm diameter mouth. The mouth was covered with a plastic 5 mm mesh to prevent the entry of predators. The jar rested on the bottom, fastened to a concrete block.

Water flowed across the mouth of the jar and suspended sediments, detritus, and metamorphosing clams settled to the bottom. In the field, the contents of the jar were washed through a 0.174 mm mesh screen. In the laboratory each sample was elutriated to remove most of the detritus (Coffin and Welch 1964). The material remaining after elutriation was examined for clams under a dissecting microscope. All bivalves were counted and some were measured. Set of bivalve species other than *Rangia* was also identified and counted.

Environmental Data

Water samples for salinity, dissolved oxygen, and temperature measurements were taken whenever biological collections were made. A Kemmerer bottle was used to obtain bottom water samples at the deep stations. Samples at shallow

stations were collected about 0.3 m below the surface. Temperature measurements were taken immediately with a stem thermometer. Bottom temperatures recorded at VEPCO instrument towers 1 and 6 (near stations A and B, respectively) were also used in this study. Salinity samples were analyzed in the laboratory with a Beckman RS7B induction salinometer. Dissolved oxygen samples were fixed immediately after collection and analyzed in the laboratory by a modified Winkler method.

Freshwater input was compiled from records taken at gauging stations on the James River near Richmond, the Appomattox River near Matoaca, and the Chickahominy River near Providence Forge. Combined, these three rivers are the major sources of freshwater for the James River in the study region.

RESULTS

Histological Study of the Reproductive Cycle

A histological basis for classifying the gonadal condition was used because the external appearance of gonads did not accurately reflect phase of development. The appearance of gonads of both sexes is superficially the same during each phase.

No evidence of gonadal parasitism was found in any of the tissue sections, nor were hermaphroditic individuals found.

There was little difference in the time of initiation of gametogenesis and ripening between the sexes so the number of males and females in each stage was combined for analyses. Figures 3 to 6 show the phases in the development of the female and male gonads.

Station A

The reproductive cycle of clams at station A (Figure 7) was more complex than at the other stations. From early February to late March 1970 most clams were in the spent phase, although a few male clams contained ripe sperm with sperm balls. In early April 1970, 40% of the sample were in the early active phase. By May, 40% were ripe, with 10% partially spawned. From May through September clams were found in all gonadal phases. Evidently some spawning and rematuration occurred during the summer months. In early October 1970, all clams examined were ripe. The volume of eggs and sperm at the second ripening was much greater than that in the early spring and summer. Partially spawned clams were numerous at the end of October and by mid-November 85% of the sample were partially spawned or spent. Throughout the rest of the winter most clams were in the spent stage, although some males retained sperm and slight gonadal activity was noted in some females.

The reproductive cycle for 1971 was basically the same as the previous year. In early June 1971, 65% of the clams were ripe. Spawning was indicated during the next 2-wk period because 60% were spent or partially spent. The fall spawning season was very similar to that of 1970, with 95% ripe by late September. Spawning was completed by early November and, again, some ripe males were observed during the winter.

Station B

Clams in the spent or inactive phase were found from February to early April 1970 (Figure 8). Some males still contained sperm in various stages of cytolysis. By late April 1970, half of those collected had begun gametogenesis, resulting in 80% being ripe by early June 1970. Clams remained in the ripe phase throughout the summer with some spawning occurring during July. During August there was a second development, resulting in all clams observed being ripe in early September 1970. Spawning commenced in early October and was completed by mid-November 1970. Immediately after spawning some clams were in the early active phase, but development did not proceed further during the winter.

The reproductive cycle for 1971 was similar to that of 1970. Gametogenesis commenced in early May. Fewer ripe clams were observed during the summer months than in 1970. The second cycle began in early July and by early September all clams were ripe. Spawning began in late October and was completed by late November. As found at station A, the second seasonal cycle for station B was more intensive; more ripe clams were found and their gonads contained far more sperm and eggs. Spawning was more intensive during the fall, with gonads progressing from ripe to spent in a month.

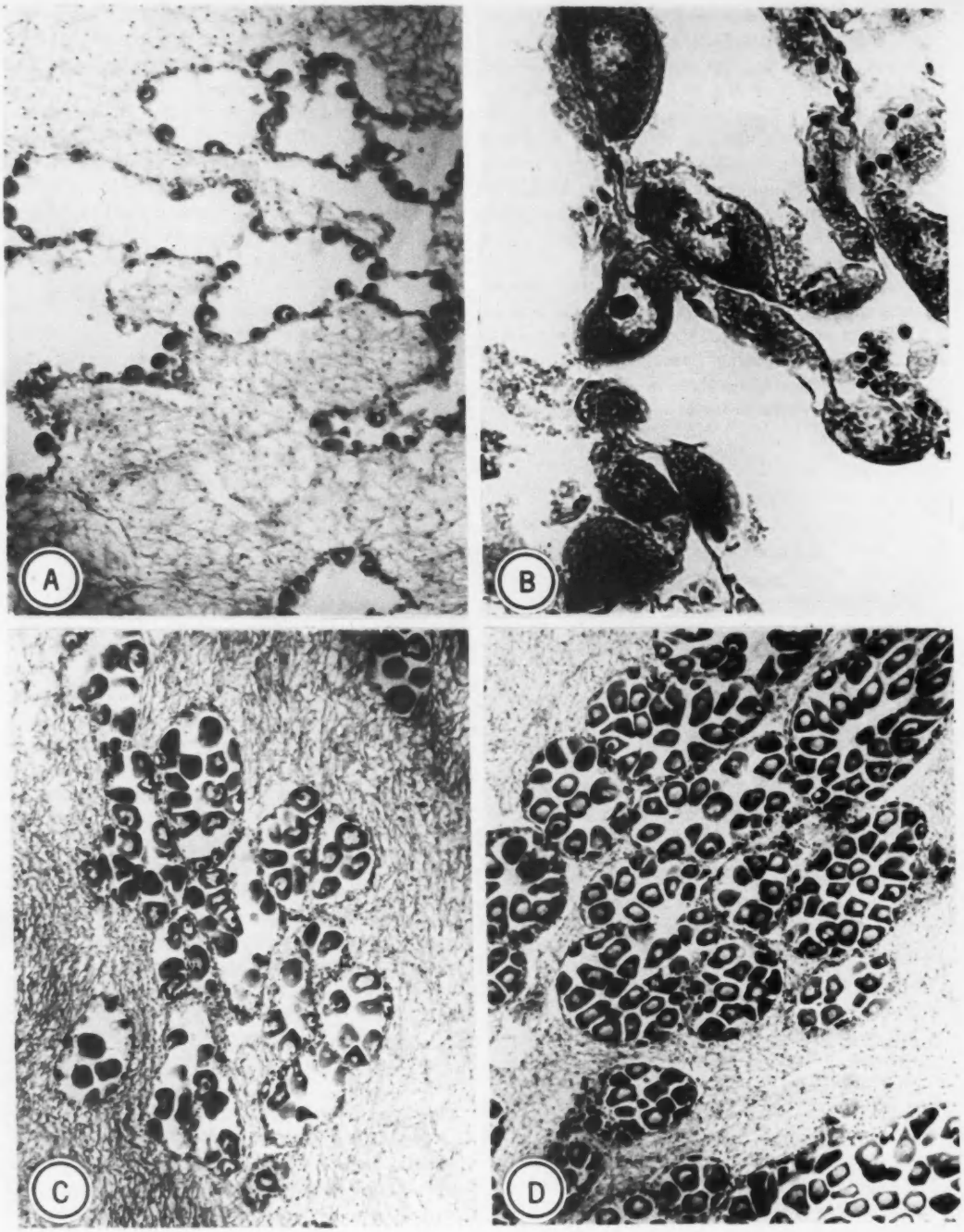

FIGURE 3.—A, section of *Rangia* ovary in the early active phase of oogenesis (× 120); B, ovary in early active phase (× 500); C, ovary in late active phase (× 120); D, ripe ovary (× 120).

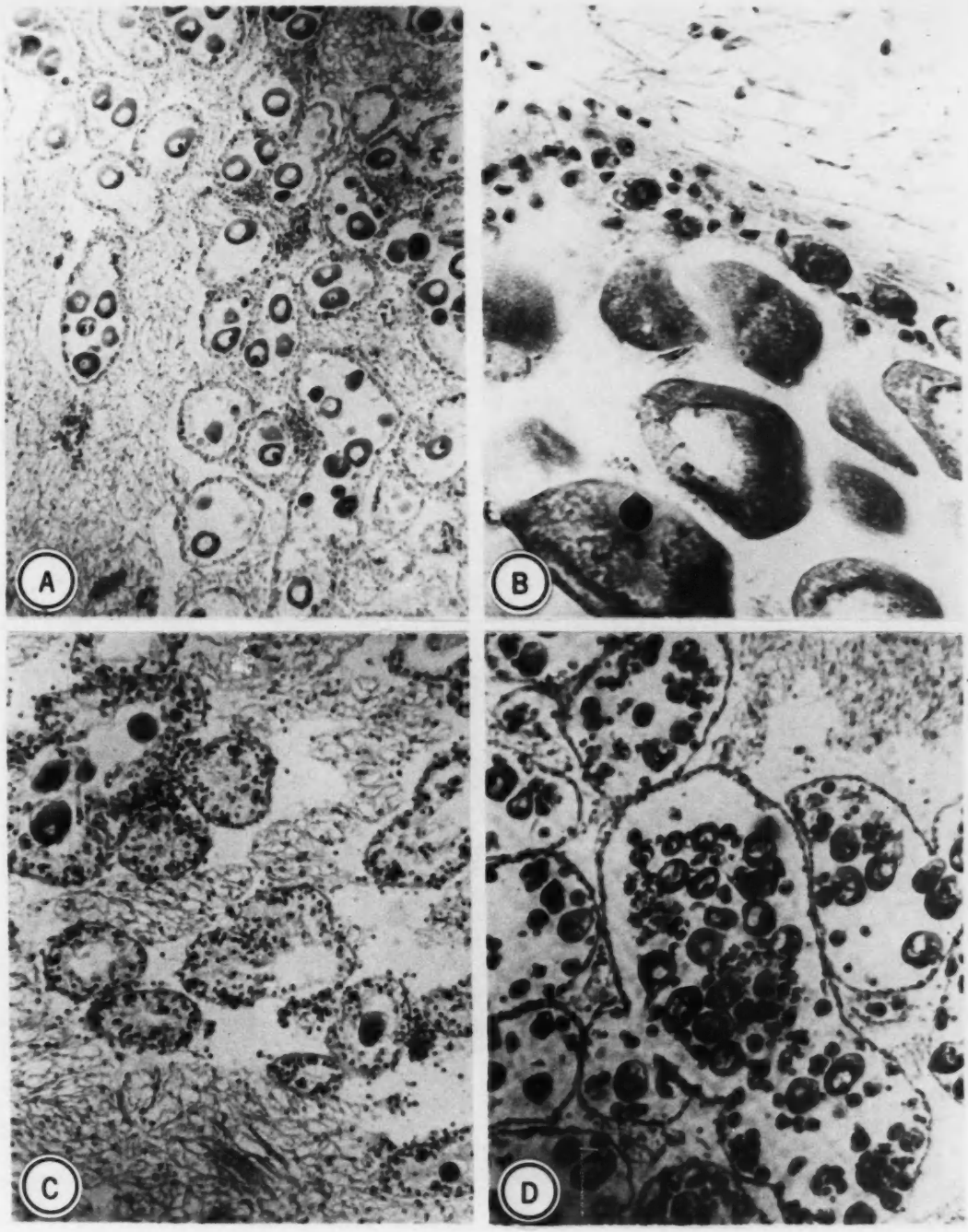

FIGURE 4.—A, *Rangia* ovary in the partially spawned phase (×120); B, partially spawned ovary (×500); C, spent ovary with few ova retained (×120); D, cytolysis of unspawned eggs (×120).

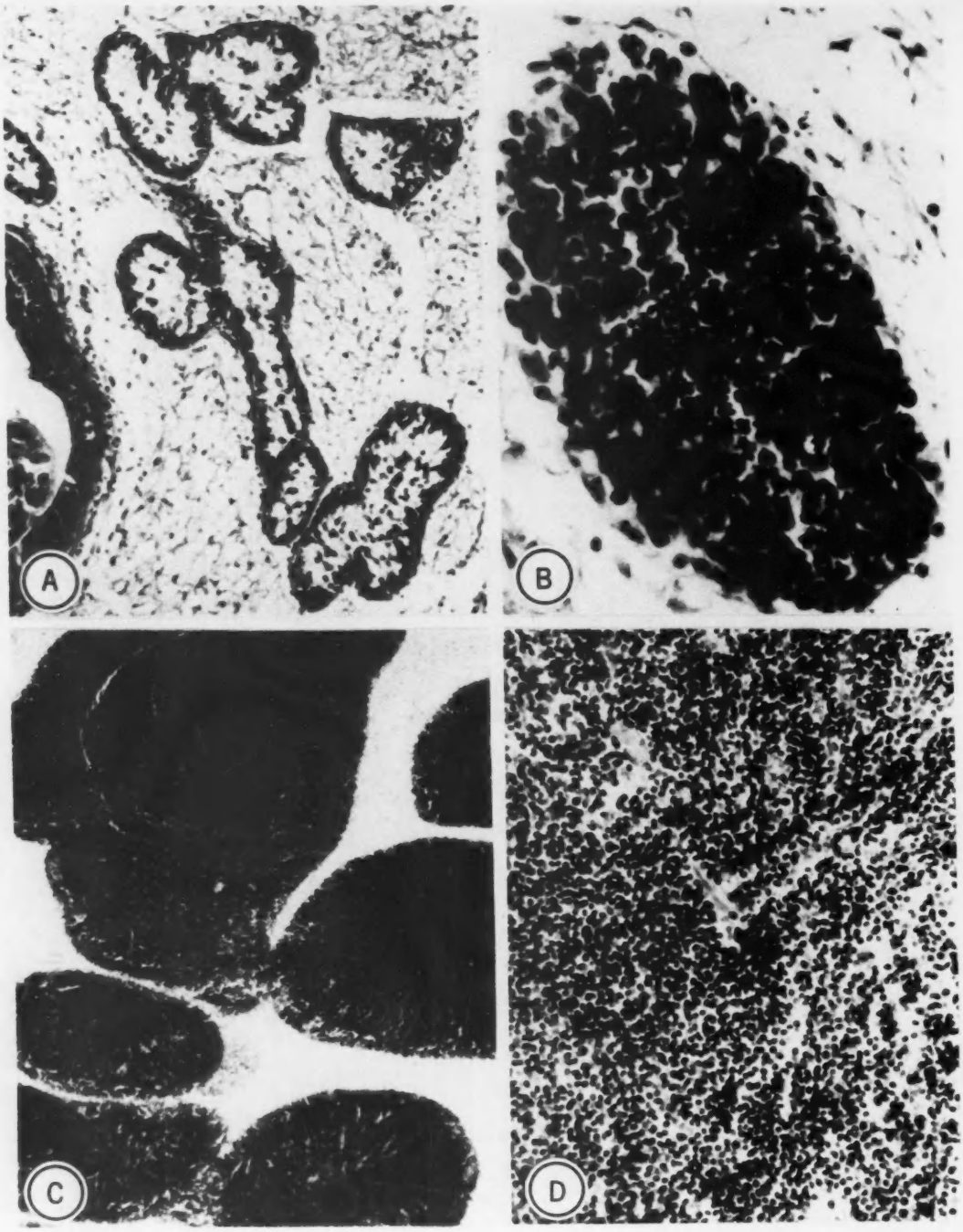

FIGURE 5.—A, Section of testis of *Rangia* in early active phase of spermatogenesis (× 120); B, testis in late active phase—note sperm in center (× 500); C, ripe male (× 120); D, ripe male (× 500).

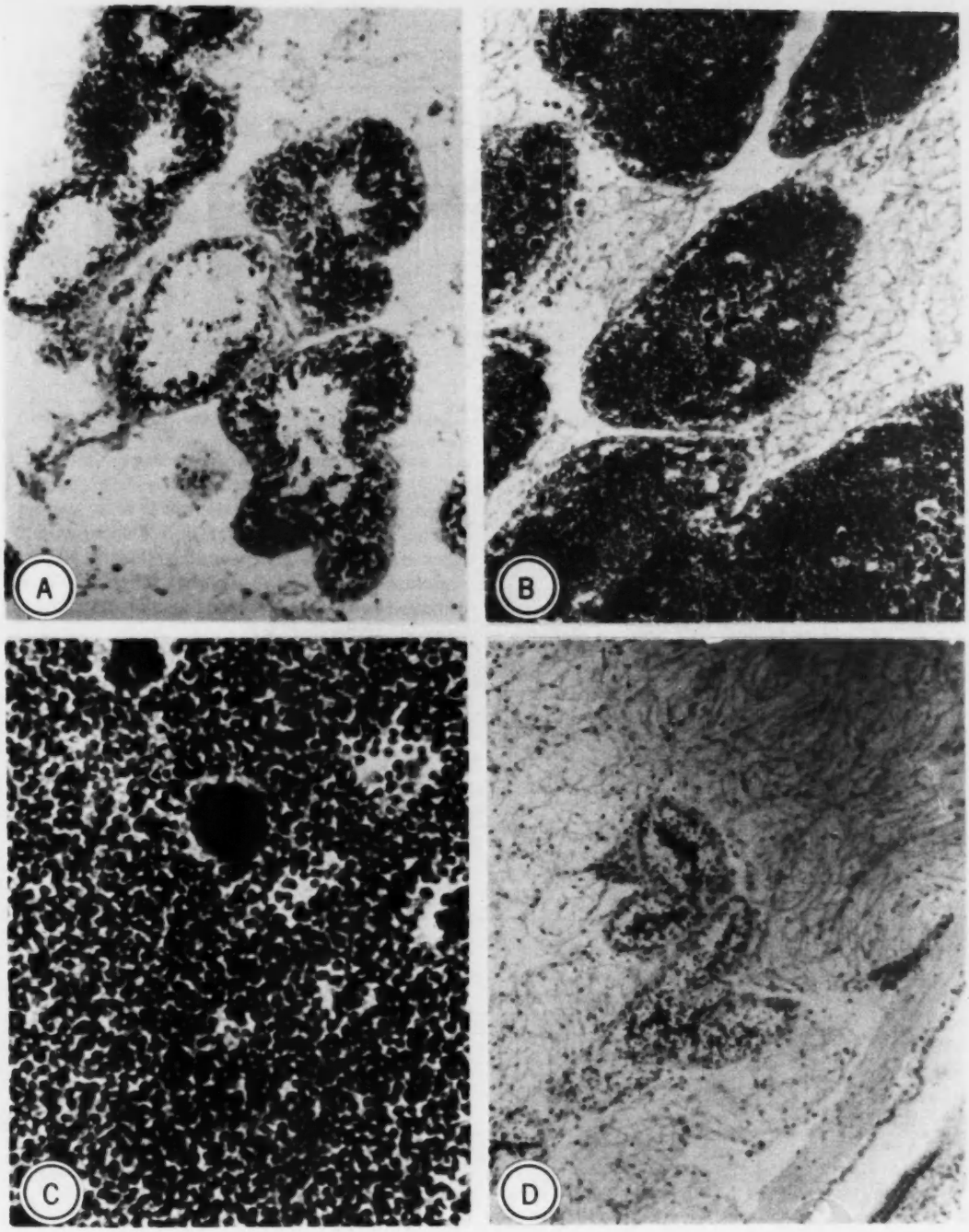

FIGURE 6.—A, Section of testis of *Rangia* in partially spawned phase (×120); B, testis with retained sperm and sperm balls (×120); C, testis with sperm balls (×500); D, spent testis with few sperm retained (×120).

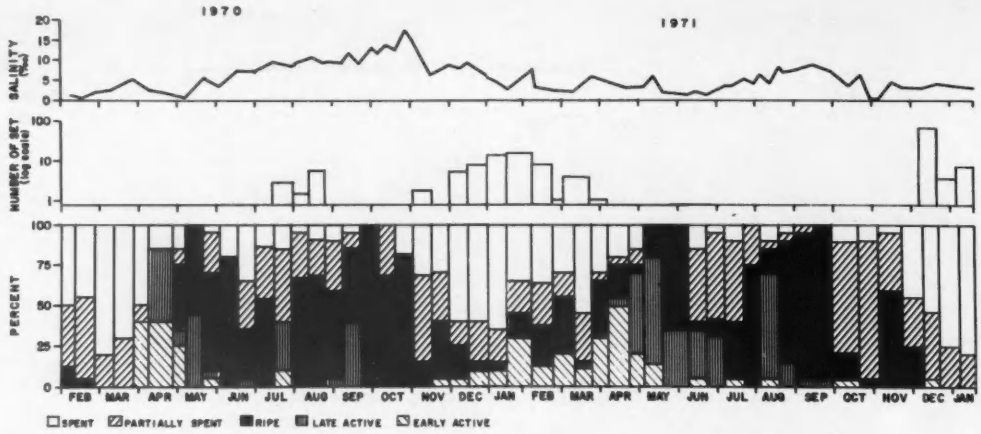

FIGURE 7.—Gonadal phases and setting of *Rangia* at station A in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

Station C

The reproductive cycle at station C was similar to that at station B during 1970. However, earlier spawning was indicated by 88% of the clams being either partially spawned or spent in early October (Figure 9). Clams remained in the spent phase until early May 1971, when gametogenesis began. Few ripe clams were found at this upstream station during the late spring and summer. Clams in the early active phase were found during July and by the end of August all clams were ripe. From September to November 1971 clams were predominantly ripe, but there was no spawning. Cytolysis of the eggs began in November, resulting in a spawned-out appearance (Figure 4D). No spawning occurred at station C during 1971, in marked contrast to stations A and B where the fall spawning was intense.

Sex Ratio

The data were divided into summer-fall and winter-spring seasons, because many clams contained no discernible gonads during the winter

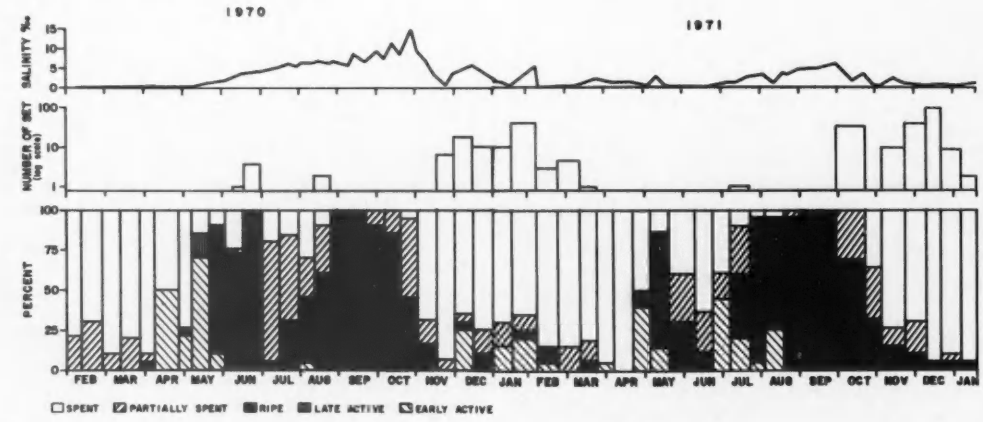

FIGURE 8.—Gonadal phases and setting of *Rangia* at station B in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

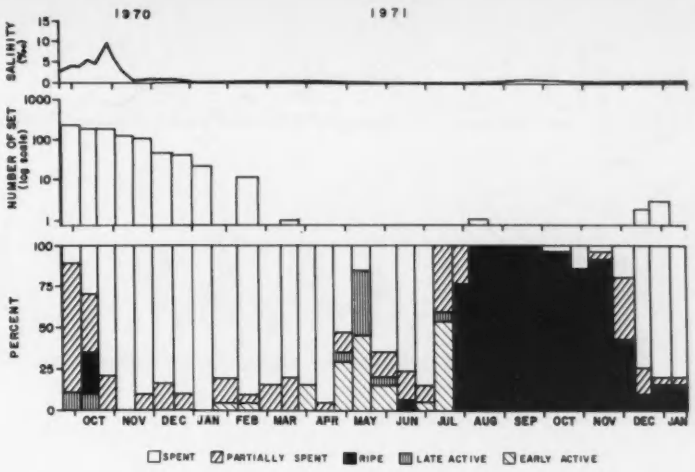

FIGURE 9.–Gonadal phases and setting of *Rangia* at station C in relation to salinity from 1970 to 1971. The length of each shaded area represents the percentage frequency of clams in each category.

and early spring. During summer and fall the gonads of most clams could be recognized (Table 1). The ratio of females to males at station A was not significantly different from 1:1. Females predominated at stations B, D, and C during the summer and fall months of 1970 and 1971. When the clams of non-determinable sex are added to the male group, there are still significantly more females.

Of the clams collected in late June 1970 at station A, none measuring 5-10 mm contained gonads. In the second group 50% showed signs of gametogenesis and had recognizable sex products; 70% of the third group had discernible gonads; and most clams in the fourth group contained gonads. Most small clams were males, but too few were examined to test the significance of sex ratios.

Larval Setting

The number of *Rangia* clams setting at each station is shown in Figures 7 to 14. This number does not provide an estimate of survival because predators were excluded by the screen cover. The number of set clams at both deep and shallow stations by season is shown in Table 2. At stations A and As a small number (< 7) set during late July and August 1970. In December 1970 through March 1971 set clams were common but not very abundant at these two downriver stations. Only one setting period (29 individuals) was recorded during the summer months at station As. Larvae began setting again during the third week of December 1971 with 70 at station A. Collectors at both stations continued receiving set until sampling was terminated on 18 January 1972.

TABLE 1.–The ratio of females to males and the number of clams with non-determinable (ND) gonads at each station. Summer and fall seasons were tested with the ND clams added to the male group.

Seasons	Station A			Station B			Station D			Station C		
	F	ND	M	F	ND	M	F	ND	M	F	ND	M
Summer and fall 1970	140	0	153ns	209	3	57**				166	9	70**
Winter and spring	61	53	83	46	128	35	13	44	13	29	118	66
Summer and fall 1971	127	7	102ns	178	22	34**	41	5	11**	138	38	54**

ns = not significant.
** = highly significant.

Setting at stations B and Bs was sporadic during the spring and summer of 1970, with no more than four clams in any jar. Setting began at station B in mid-November 1970 and continued there until late March 1971. A maximum of 42 individuals was collected on 8 February 1971. Set clams were found on only one sampling date during the next summer. Setting in the fall began in late October 1971, with very large numbers during late November and early December.

Setting at station D was similar to that at station B except more individuals were found during the fall and winter of 1970-71. One hundred eighty-five were collected in the station D bottle in mid-December 1971.

Only data beginning in September 1970 were available from station C. As noted in the tissue sections, spawning had commenced earlier. Setting from early September 1970 to March 1971 was very heavy, with 257 clams collected at this station

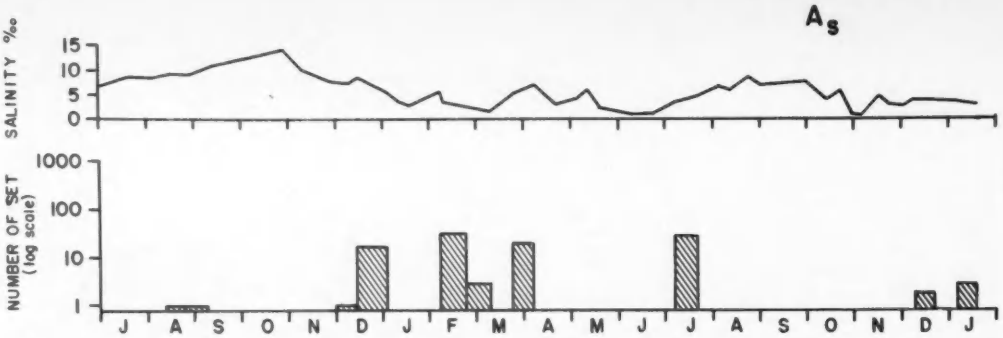

FIGURE 10.–Number of *Rangia* set and salinity at station A_S from July 1970 to January 1972.

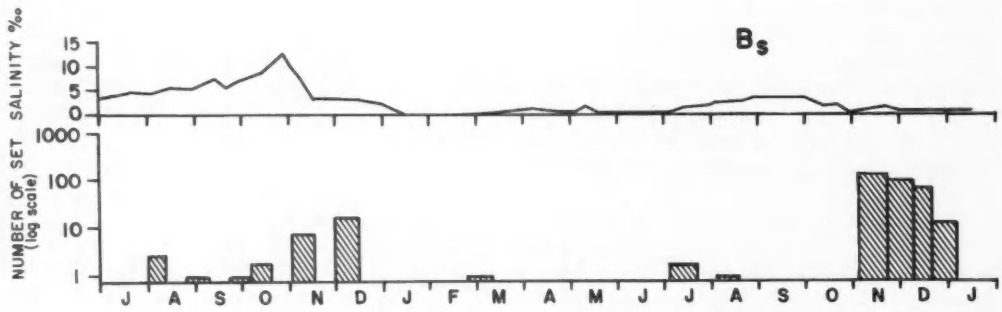

FIGURE 11.–Number of *Rangia* set and salinity at station B_S from July 1970 to January 1972.

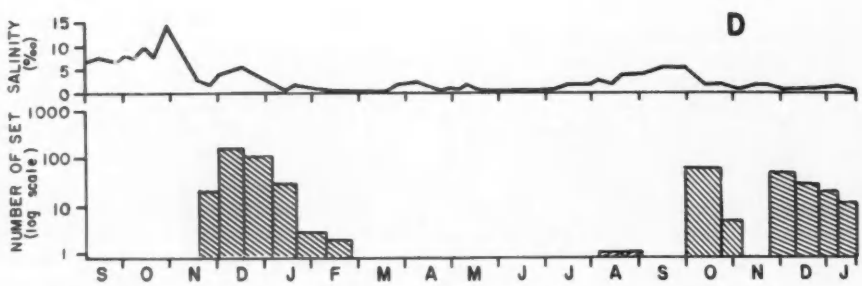

FIGURE 12.–Number of *Rangia* set at station D in relation to salinity for September 1970 to January 1972.

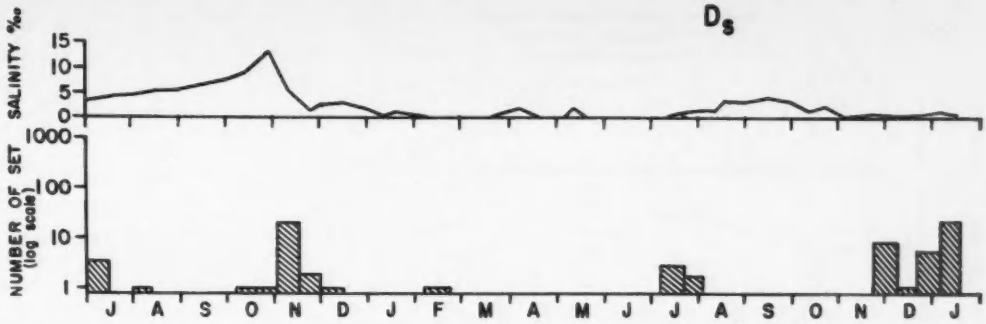

FIGURE 13.—Number of *Rangia* set and salinity at station D_s from July 1970 to January 1972.

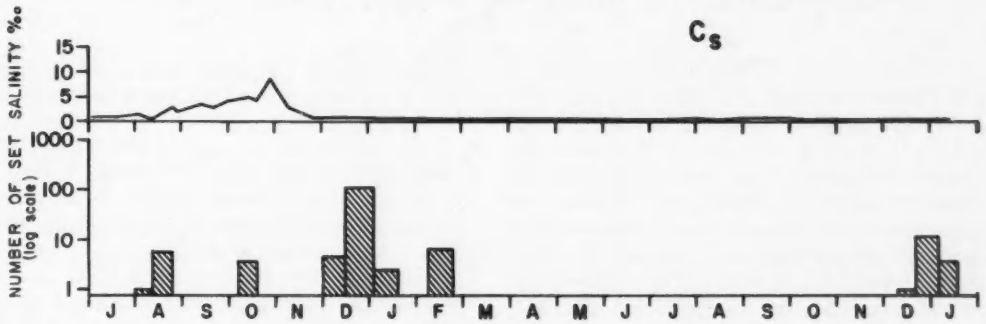

FIGURE 14.—Number of *Rangia* set and salinity at station C_s from July 1970 to January 1972.

TABLE 2.—Average number of *Rangia* set (per collector) at both deep and shallow stations by season.

Season	Station			
	A	B	D	C
Summer (1970)	0.7	0.7	0.7	—
Fall-winter	3.6	6.1	25.5	74.3
Summer (1971)	1.6	0.2	0.4	0.1
Fall-winter	6.2	44.9	15.4	2.5

by early October 1970. This was the highest number collected at any time or place during the study. No set was collected at stations C or Cs from late March to late December 1971. The fall setting was very small with only 5 collected at station C and 18 at station Cs during December 1971 and January 1972.

Rangia set ranged in length from 230 to 500 μm, but averaged about 300 μm. Larger individuals were generally collected at the shallow stations but may have been members of an earlier set washed in by wave action.

The setting patterns of the other bivalves are presented in Figure 15. Station A received more set of all three species than the other stations because of its proximity to their adult populations. *Brachidontes recurvus* and *Macoma mitchelli* were collected farther upriver than *M. balthica*. The first two species were common at stations A, B, and D. *Brachidontes recurvus* and *M. mitchelli* are evidently more tolerant of low salinities as they were the only set found during the low salinity conditions of fall 1971. All three species have a nearly year long spawning season with minor spring peaks and a major peak in the fall.

The three most common organisms found on the bottles were *Rhithropanopeus harrisii*, *Callinectes sapidus*, and the blenny, *Chasmodes bosquianus*. These three potential set predators were typically found at stations A, B, and D during the fall and winter months. During high salinity periods, *R. harrisii* was found at station C.

Hydrographic Data

Freshwater input levels were usually high in late winter and spring, declining to low levels in late summer and fall (Figure 16). Flow during the

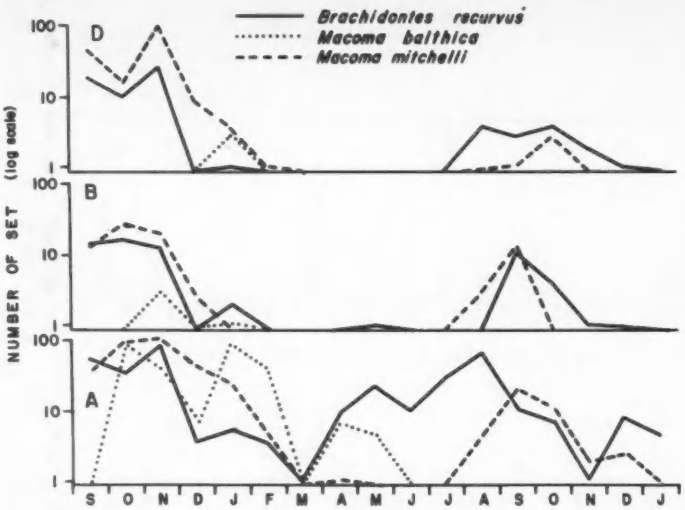

FIGURE 15.–Setting patterns of other bivalves at stations A, B, and D from September 1970 to January 1972. Data combined at deep and shallow stations.

fall of 1970 was very low, with about 28.32 m^3/s (1,000 cfs) input in September and October. This low input allowed measurable-salinity water to extend as far upstream as mile 45. Input was high and variable during the winter and early spring of 1971. The peak for the 2-yr period of 2,747 m^3/s (97,000 cfs) was recorded on 1 June 1971. The summer input was fairly low but quite variable and river flow during September and October was considerably higher than the previous fall. The salinity was rarely measurable at station B throughout the fall and winter months of 1971.

The annual temperature pattern for station B (Figure 17) is representative of the study area. Within relatively narrow limits, all deep stations exhibited similar temperature profiles. Lowest temperatures were measured during late January and early February, followed by a relatively smooth increase to a maximum of 29°C during early August. A period of stable high temperatures was recorded from June through September.

Dissolved oxygen concentrations in this region

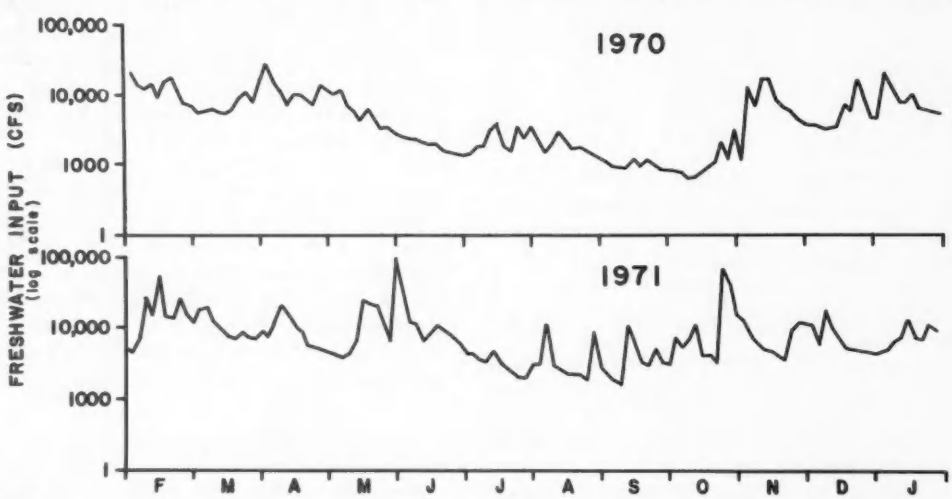

FIGURE 16.–Freshwater input into the James River at 4-day intervals. The data include input from the Appomattox and Chickahominy Rivers.

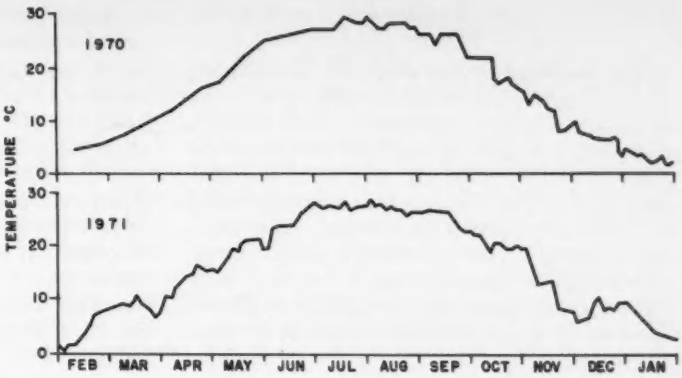

FIGURE 17.—Bottom water temperature at station B in the James River, Va. Values taken from VEPCO instrument tower (#6) and bottom water samples.

showed the normal seasonal variation, with the highest concentrations in the early part of the year during the low-water-temperature period. Low values (6-8 mg/liter) were recorded for deep stations during the summer months.

Relationship of the Reproductive Cycle to Environmental Data

At station A, gametogenesis started when the water temperature was near 10°C in the spring of 1970 (Figure 7). Ripe clams were first observed when the water temperature was 16°C and spawning was first noted when the salinity was between 3 and 5‰. Gametogenesis and spawning occurred through the summer period of high salinities and high temperatures. The fall spawning started at the highest salinities of the year with a definite major spawning after the salinity dropped 10‰ (Figure 7). The temperature during the fall spawning was 13°-15°C. Set first appeared the second week in November and occurred throughout the winter months. Fall and winter sets generally were accompanied by temperatures below 10°C and occasionally to 1°C. Gametogenesis was in progress again by the time the water temperature reached 15°C. No set clams were collected during the summer of 1971, although the histological sections showed all stages of development. Salinities and temperatures approximated those of the previous year, although salinity was more variable. Renewed gametogenesis coincided with the highest temperature of the summer and rising salinities. Some spawning took place with the declining salinity, but the major spawning occurred near 5‰.

Gametogenesis at station B started almost 2 wk later than at station A in the spring of 1970, with the temperature above 13°C (Figure 8). Ripe clams were similarly noted nearly 3 wk later than at station A. The salinity during the summer months was near 5‰ and gradually rising. There was little agreement between spawning times as noted in the histological sections and setting in the collectors during the summer. The progression of gonads in the fall from ripe to spent was clearer and more defined at station B than at station A. Spawning commenced when the salinity reached the yearly high and peaked when the salinity fell rapidly from 15 to 1‰. Setting took place 2 wk later and continued into the winter. Temperatures during spawning ranged from 22° to 12°C. Fewer clams were in the ripe phase throughout the summer of 1971 when the water was nearly fresh. More clams became ripe as the salinity increased, but few set were collected all summer at this station. Fall spawning commenced at 22°C and 6‰ and continued until the salinity reached approximately zero and the temperature dropped to 17°C. Some set were collected immediately after salinity decline and setting continued into January 1972.

Spawning was completed at station C by the end of October 1970, after salinity had fluctuated from 0 to 5‰ for the previous 2 mo. Setting began at temperatures above 25°C and continued throughout the winter at low water temperatures and low salinities (Figure 9). The salinity at station C remained below 1‰ until the termination of the study in January 1972. There was very little spawning and setting at station C during the low salinity period even though gametogenesis took place normally.

DISCUSSION

The histological examination of gonads indicates several generalizations about the reproductive cycle of *R. cuneata*. Gametogenesis began in early April and continued throughout the summer months. Ripe gametes were observed from May to late November. A slight spawning peak was noted during the summer, but a major spawn occurred in the fall. This was probably not a second cycle because gametogenesis in most cases had not terminated during the summer; instead, it appeared to be a continuation of gamete development at an increased rate.

The gametogenic cycle of *Rangia* in high and low salinities was basically the same. Temperature appeared to be the more important stimulus in initiating gametogenesis in the spring and summer. A temperature of approximately 15°C coincided with initiation of gametogenesis at all stations. Gametogenesis in clams from freshwater occurred at a slower rate during the spring and summer with more clams in the spent phase than at the other localities.

The reproductive cycle as determined in this study is similar to that reported for *Rangia* in other geographic areas. Fairbanks (1963) indicated that in Lake Pontchartrain, La., ripe clams could be found during March, April, May, and in the late summer and fall. A prolonged spawning season would seem reasonable as the rise in water temperature to 15°C in the spring is nearly 2 mo earlier at that location than in the James River. In addition, the drop in water temperature to 15°C in the fall is later. He also indicated a postspawning recovery phase during midsummer. The very high temperature (near 33°C) during the summer may have inhibited gametogenesis, but in the James River population a renewed surge occurred at the high midsummer temperatures of 28°-29°C. Tenore (1970) studying the macrobenthos of the Pamlico River, N.C., found *Rangia* containing mature gametes only in the fall. This observation was probably based on visual inspection of the viscera. The spring and summer ripening may have been missed because the gonads are not nearly as distended and colored as in the fall ripening. Pfitzenmeyer and Drobeck (1964) collected *Rangia* in August and September from the Potomac River. Clams at this time contained mature gametes, indicating that spawning was imminent.

The correlation of the environmental data to gonadal conditions suggests that temperature and salinity are important factors in spawning. Salinity, however, was more important than temperature. Clams upstream at station C spawned in fall 1970 following a 5‰ rise in salinity, but failed to spawn in 1971 when the salinity remained low. Spawning at station B was apparently related to salinity decreases. The correlation of salinity to spawning was not as clear at station A. The salinity variation at this station was very large over a tidal cycle and may have prevented complete synchrony of spawning.

Cain (1973) found that a salinity change was necessary for *Rangia* spawning in the laboratory. Spawning was accomplished by placing ripe clams from low salinities (< 1‰) into 5‰, 28°C flowing water. Evidently clams in upstream areas require a rise in salinity to spawn, while downstream populations require a reduction in salinity from the 10 to 15‰ levels at which they live.

There is little additional evidence in the literature on the importance of salinity to *Rangia* spawning. Fairbanks (1963) could not induce spawning. Chanley (1965) induced spawning at 15 ‰ by rapidly increasing the water temperature 7°C and adding sperm stripped from a ripe male. However, spawning was poor and he did not study the survival of the eggs. Such strong stimuli may cause premature release of immature eggs, with subsequent poor fertilization and survival. The only data suggesting the importance of salinity to *Rangia* spawning is that from the Bureau of Sport Fisheries and Wildlife (1965) in connection with a study on the food habits of ducks in Back Bay, Va., and Currituck Sound, N.C. These two bodies of water normally have a salinity of less than 1‰. During that study, a storm forced ocean water into the bay and raised the salinity to about 4.5‰. This intrusion of salt water must have caused spawning and successful setting since the following year nearly 9% of the diet of dabbling and diving ducks consisted of small *Rangia*, an amount estimated to be 83,000 lb (dry weight) for the year. During the previous 3 yr no *Rangia* were consumed by these ducks.

Two periods of setting occurred in the James River. The first was in early and midsummer, which coincided with the beginning of spawning as inferred from tissue sections. The second period was much longer, with a greater number of collected set, and took place in the late fall and winter, coinciding with the increased percentage

of partially spawned and spent clams, as identified by histological preparations. The second peak of spawning appeared to be the major one for the normal reproductive period (Table 1). Fairbanks (1963) found set (>0.375 μm) from October to April. A longer and more intense setting period was found in the area with the more variable salinity. Tenore (1970) collected set in bottom grabs only during the fall and winter months. The spring and summer spawning was either so light in these areas that no set were found or an abundance of predators at this time quickly consumed the sparse set.

Sex Ratio

There are at least two possible explanations for the unusual sex ratios in *Rangia*. *Rangia* may be protandric with a higher ratio of females to males in the older stages. If so, the clams at stations B, D, and C would have had to be older than those at station A; however, there were no consistent differences in the lengths of the clams at the various stations. This does not preclude the possibility that the ages of clams at the stations are different, but masked by varying growth rates resulting from substrate effects or nutrient levels.

The second possibility is that the environmental conditions upriver differ enough from those downriver at station A to affect the sex ratios. Changes in environmental factors could affect either juveniles or adults during the undifferentiated period. There is no proof of this type of sex alteration. None of the other mactrids studied, *M. lateralis*, *S. solidissima*, or *T. capax* have been found to have a ratio other than 1:1.

Relationship of Larval Studies to Setting

Cain (1973), on the basis of laboratory results, indicated that best survival and growth of larvae would be expected in the summer. Higher temperatures and generally high salinities are expected to provide for rapid growth to setting. But setting is very poor in summer (Table 1). A number of factors may account for this: clams are in all stages of gametogenesis, the gonads of ripe clams are not as full, and even though the stimulus to spawn may exist there is probably poor synchrony of spawning.

In the James River, fall and winter were the times of greatest setting activity. Fall spawning occurred as the temperature dropped from 29° to 15°C. This temperature range would provide good survival of eggs to straight-hinge larvae, but the larvae are exposed to declining fall temperatures. Larvae at low temperatures (and low salinity) should survive well, but grow slowly. Consequently, set in the late fall and winter come from a fall spawning after the delay in growth and metamorphosis expected from low temperatures. Some set in the jars could have come from previously set, slow-growing clams washed in by turbulence. This set, which is fairly active, tends to crawl over the bottom by use of the muscular foot and therefore is affected by currents (Carriker 1961).

Distribution and Recruitment of *Rangia* in the James River

Rangia extends to nautical mile 60 in the James River. In the upper reaches of its distribution it has been in freshwater for the last 4 or 5 yr. Since the embryos and early straight-hinge larvae cannot tolerate freshwater (Cain 1973) and a salinity rise is needed to induce spawning, there must be little recruitment to this population. No set or small clams have been found in this area, which raises the similar question of how *Rangia* spread into this region initially. The upriver population consisted of clams ranging in length from 53 to 63 mm in the spring of 1971. Using the von Bertalanffy growth curve constructed for *Rangia* by Wolfe and Petteway (1968), these clams were estimated to be from 5 to 7 yr old. The water records for the James River basin were analyzed from 1963 to 1966 (Anonymous 1966, 1970b). These records show yearly lows in the late summer and fall when the input dropped below 22.66 m^3/s (800 cfs), and in 1966 the input dropped to an average of 13.59 m^3/s (480 cfs) during the first half of September. These very low flow periods allowed measurable-salinity water to extend 63.5 miles upstream in December 1965 (Brehmer and Haltiwanger 1966).

To reach these upstream areas larvae must be transported in the more saline bottom water which has a net upstream movement (Pritchard 1952; Nichols 1972). Although the mechanism of such transport has not been deduced for *Rangia*, work done on the eastern oyster may indicate some possible mechanisms. Wood and Hargis (1971), who studied the lower James estuary, found a definite upstream transport of oyster larvae and

also of small coal particles. They indicated that the larvae move upstream by selectively swimming in more saline water associated with the flood tide. They further indicated that Korringa's (1952) idea of passive transport could not be denied, as the coal particles also had a net upstream motion. *Rangia* could be carried into upstream areas both by selective swimming or by passive transport under low flow conditions, and a series of dry years would allow set to progressively move upriver. Set from one year should be able to spawn the next year and certainly within 2 yr. Gonads occurred in clams 14 mm long, a length easily reached by the end of the first year (Fairbanks 1963; Wolfe and Petteway 1968). Rapid early growth and a relatively short larval life (above 20°C) should allow for the fast spread of set into areas uninhabited by adults. As *Rangia* has an 8-yr average life span (Fairbanks 1963) and a maximum life of 14 yr (Wolfe and Petteway 1968), recruitment to the population could occur at fairly long intervals. The Virginia Division of Water Resources (Anonymous 1970a) statistically predicts that low flows of less than 1,000 cfs for 7 days will occur at 5-yr intervals. This situation could allow minimum recruitment to maintain the upstream population, assuming good survival of set and adults in this region.

The downstream extent of *Rangia* could be determined by the adults approaching their high-salinity limit. This may not be the case as the larvae can survive higher salinities than normally occur at the downstream limit—and the adults may also do so. The downstream extent likely represents a multifactor barrier involving biological competition for space and food, and increased predation of the set.

Recruitment to the downstream population was at a low level but more regular, with more set collected in the summer months than at the upstream stations (Table 1). Probably the best recruitment would be expected in the population at station B near the lower middle of the habitat range. The fall set there was high and fairly consistent over the 2-yr period. Averaged over many years, this segment would likely receive more set, as this part of the estuary usually has an annual salinity change from fresh to 5‰.

General Discussion

The adults can utilize the high levels of detritus in this oligohaline sector (Darnell 1958) and convert it into growth and reproductive materials. *Rangia* is ripe for at least 7 mo of the year so it can spawn whenever favorable changes in salinity allow successful reproduction. Although adults are euryhaline, embryos are much more sensitive. Spawning at a salinity near 5‰ allows for the survival of the sensitive stages to the more eurytopic later larval stages. The increased tolerance of the larvae permits good survival during its more stressful pelagic existence.

The planktonic existence of *Rangia* larvae is greatly extended by low temperatures. Thorson (1946) indicated that prolonged low temperatures exposed larvae to increased mortality from disease, starvation, predation, dispersion, and environmental stress. *Rangia* larvae evidently are well adapted to a prolonged exposure because many set were collected during the coldest months. This increase in dispersal may allow *Rangia* to consume the unexploited resources of the species-poor environment in low salinity. Increased dispersal may also provide genetic interchange between populations distributed over a relatively extended habitat in the estuary. Pfitzenmeyer and Drobeck (1964) found the rate of increase of *Rangia* over a 4-yr period in the Potomac River to be very great. Pfitzenmeyer (1970) also recorded this clam in the upper Chesapeake Bay when its numbers increased from 0 to 10,000 per square meter in 2 yr.

Spawning of *Rangia* apparently is controlled by salinity change. The mechanism of this control, however, has not been examined. The exogenous factor of salinity may activate an endogenous control system of osmoregulation and serve as a signal to induce synchronous spawning of the population. The concept of "critical salinity" reviewed by Khlebovich (1969) appears operative for *Rangia* which spawns near 5‰. Khlebovich concluded that the salinity range of 5-8‰ is a faunal boundary defining the distribution of marine and freshwater species. Characteristic differences in physiological performances (adaptation, growth, activity and, especially, osmoregulation) are revealed at this salinity range.

The latitudinal distribution of *Rangia* is important because of its spread northward in the last decade. In the present study, gametogenesis and spawning were observed to occur over a wide range of temperatures. Although larval growth was best at high temperatures, survival and growth apparently take place even at low temperatures. Consequently, it appears that the

northward limit of *Rangia* is not controlled by low temperature effects on reproduction or larval tolerance. Reports on populations in upper Chesapeake Bay (Gallagher and Wells 1969; Pfitzenmeyer 1970) infer large adult mortalities from low temperature and low salinity. The only mortality of adults (freshly gaped clams) in this study was seen in the dredge hauls during the winter and early spring. Long periods of low temperature and freshwater may combine to increase the mortality of adults and thereby limit the northward range.

The possibility that widely separated populations may belong to different physiological races cannot be excluded (Loosanoff 1969). Populations of marine animals exposed to different environments within their geographical range may have different physiological properties (Sastry 1970), suggesting that more research should be conducted on the tolerances of embryos, larvae, and adults from different geographical areas.

The key to the welfare of a *Rangia* population over its normal distribution is probably not the physiology of the adult individual but successful reproduction and recruitment. Adults may live for years in habitats where reproduction is impossible. Spawning will not occur unless salinity changes, up from low salinity or down from high salinity. If spawning does occur, embryos and early larvae will have poor survival unless salinity is between 2 and 10‰ (Cain 1973). Once the larvae have developed past the swimming stage and settled to the bottom as juvenile clams, salinity is probably not as critical (except in combination with low temperatures).

The influence of salinity on reproduction and recruitment indicate that some changes in its environment may restrict the distribution of *Rangia* in the estuary. *Rangia*'s estuarine distribution is maintained by changes in salinity related to variations in the freshwater input. Any overall reduction in freshwater input or reductions in the seasonal variations of salinity will limit its range. These characteristics of this species should be considered before dams are constructed, freshwater is diverted for other uses, or other changes in the hydrography of the estuary are approved.

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HORMONAL-INDUCED OVULATION OF THE WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*

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ABSTRACT

The response of winter flounder, *Pseudopleuronectes americanus*, to human chorionic gonadotropin (HCG), oxytocin, pregnant mare serum gonadotropin (PMSG), deoxycorticosterone (DOCA), and freeze-dried carp pituitary is described. HCG and PMS were successful in some instances in producing viable eggs and larvae while carp pituitary was successful in all instances. These were the first known successful attempts to induce maturation and spawning of winter flounder artificially in the laboratory.

Larvae obtained from these hormonal-induced spawnings were normal in all respects and were reared in the laboratory through metamorphosis. Wild plankton obtained from Narragansett Bay, brine shrimp nauplii, and chopped clams were fed as food. The early life history of this flatfish can, for the first time, be completed under controlled laboratory conditions.

The winter flounder, *Pseudopleuronectes americanus* (Walbaum), an important species in local New England commercial and sport fishing industries, occurs from Chesapeake Bay to the northern shore of the Gulf of St. Lawrence (Bigelow and Schroeder 1953). Winter flounder spawn from January through April in Rhode Island estuaries with a peak spawning period in February. Demersal eggs are produced which range from 0.74 to 0.85 mm in diameter.

Investigations to evaluate methods of inducing spawning of winter flounder with the aid of hormones under controlled laboratory conditions were undertaken at the National Marine Fisheries Service, Northeast Fisheries Center, Narragansett Laboratory in 1970 and continued over a 3-yr period. The use of hormone injections for inducing spawning in other species of fish has been well documented by Pickford and Atz (1957). The induction of spawning in winter flounder in the laboratory provides a practical method of supplying viable eggs and larvae for physiological studies. By controlling water temperatures, photoperiods, and injecting hormones, the research time for this species can be extended. As far as is known, these were the first reported successful attempts to artificially mature and spawn the winter flounder in the laboratory.

MATERIALS AND METHODS

Adult winter flounder were captured by otter trawling in Narragansett Bay in the autumn of 1970, 1971, and 1972, and were brought to the Narragansett Laboratory in a 380-liter live car equipped with an aerator. In the laboratory, the fish were held in 1,890-liter circular aquaria (1.2 m in diameter; water depth, 0.8 m). A continual supply of filtered seawater was pumped to the aquaria from Narragansett Bay.

After acclimating in the laboratory, the fish were segregated by sex, measured and weighed, and tagged with numbered plastic pennants secured through the caudal peduncle with a double barbed stainless steel wire. Winter flounder adults may be sexed easily by placing the fish on its back and running a hand down the white underside. Females are quite smooth while the males are very rough to the touch. Winter flounder lend themselves quite readily to handling and have proven to be a durable fish. No anesthesia was required prior to injecting hormones as the fish rarely struggled.

An artificial photoperiod of 9 h light and 15 h darkness (9L:15D) simulating seasonal light conditions was maintained for all experiments by time clocks controlling four banks of 80-W cool white fluorescent lights suspended 1.2 m above the tanks.

Since winter flounder fast during the spawning season, as many other fish do, their food regimen was not difficult to maintain. A varied diet of clams, squid, chopped menhaden, and silversides

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was provided. Very few females fed actively. However the males, a majority of which were running ripe, fed throughout the experiments.

Hormone injections were carried out with 0-2 cc syringes fitted with 20 gauge, 3.85 cm (1.5 inch) needles. All injections were intramuscular. Intraperitoneal injections were ruled out for fear of injuring or killing the experimental fish. Injections were made into the back muscle below the dorsal fin. Inserting and withdrawing the needle slowly aided in retaining most of the fluid in the fish (Figure 1). After injection, the flesh of the fish was massaged to diffuse the fluid into the muscles. A saline solution of isotonic sodium chloride was used as a carrier for all hormone injections except with deoxycorticosterone, which was mixed with sesame oil and injected as a slurry. Hormones tested in the various studies were: human chorionic gonadotropin (HCG), oxytocin, deoxycorticosterone (DOCA), pregnant mare serum gonadotropin (PMSG) and carp pituitary (freeze-dried powder). The criteria chosen to test the effectiveness of the hormones were gonad index, spawning, fertilization of eggs, and hatching success. Hormones were prepared on the day of injection, and dosages were established by the weight of each individual fish.

FIGURE 1.—Winter flounder receiving hormone injection.

Running ripe fish were stripped by hand. Winter flounder spawn adhesive demersal eggs which form clumps under experimental conditions. Spawned and fertilized eggs were handled and treated according to the separation techniques of Smigielski and Arnold (1972).

Human chorionic gonadotropin was the first hormone selected for evaluation. Stevens (1966) reported successful spawnings of striped bass with dosage levels of this hormone ranging from 31 through 403 IU/pound fish. Two hormone dosage levels and two time sequences of injecting were administered to three groups of test fish numbering five per group at dosage levels of 150 IU/454 g fish injected daily, 300 IU/454 g fish injected daily, and 300 IU/454 g fish injected every other day. A fourth group served as controls. Water temperatures during the first testing trial ranged between 5° and 7°C with a mean of 6.2°C.

A second series of experiments was initiated when the water temperature fell to 4°C. Water temperatures during these trials ranged between 3° and 5°C with a mean of 3.2°C. A test group numbering 15 fish was established and held in three 1,890-liter aquaria. Dosage levels of 150 IU/454 g fish were dispensed daily and administered over a time period of 12 days.

Further experiments were initiated to evaluate oxytocin, DOCA, and PMSG at the two water temperature ranges of 6°-7.5°C and 3°-5°C. Mean water temperatures during the trials were 7.2° and 3.2°C. Because of variable results obtained with the hormone HCG in prior experiments, HCG was included in these trials for further testing. Three dosage levels of each hormone were evaluated and a total of five injections administered over a period of 10 days. The dosage levels were: oxytocin at 10, 20, and 40 IU/454 g fish; DOCA at 5, 10, and 20 mg/454 g fish; PMSG at 55, 110, and 220 IU/454 g fish; and HCG at 100, 200, and 400 IU/454 g fish. Female test fish were measured, weighed, tagged, and placed into four 1,890-liter circular tanks supplied with a continual supply of seawater. Each tank contained a total of

16 fish. The three differing dosage levels of each test hormone were injected into groups consisting of four fish per group, and the remaining four fish in each tank served as uninjected controls. At the termination of the trial, test fish were sacrificed, ovaries examined, and gonosomatic index (GSI) levels recorded.

A final series of experiments was initiated to evaluate the effectiveness of carp pituitary (freeze-dried powder) at the dosage levels of 5.0 mg and 0.5 mg/454 g fish injected daily. Two groups of test fish with each group consisting of three trial fish and three uninjected controls were established and held in two 1,890-liter tanks. During the trials, water temperatures ranged between 1.5° and 3.5°C with a mean at 2.5°C.

RESULTS AND DISCUSSION

In the group of test fish that received HCG injections at 300 IU daily, one fish hydrated after a single injection (Table 1). Hydration, an increase in total body weight due to water uptake by the ovaries resulting in higher GSI levels, was rapid, and the following morning this fish was grossly bloated. Externally, hydrated fish may become slightly swollen or grossly bloated. The majority of the eggs stripped were opaque and misshapen, and approximately 5% of the total egg mass in the ovaries were viable. These eggs, numbering approximately 10,000, were fertilized but embryonic development ceased in the blastula stage and none survived to hatch. This rapid hydration may have been responsible for the poor quality of the eggs. A long development period for oocytes with a minimum of 2 or 3 yr from the time oocytes become histologically recognizable until they are spawned has been suggested for winter flounder by Dunn and Tyler (1969). Our observations in the past have noted that the natural hydration and ovulation process of winter flounder can occupy a lengthy period of time (unpubl. data). The remaining fish in this test group were refractory after receiving a total of 12 injections.

TABLE 1.–Effects of human chorionic gonadotropin (HCG) on *Pseudopleuronectes americanus*, temperature range 5°-7°C (± 6.2°C). Photoperiod 9L/15D.

Hormone and dosage	No. of fish	No. of injections	Number hydrated	Number ovulated	Fertilization (%)	Hatch (%)
300 IU HCG/454 g fish daily	1	1	1	1	[1]5	0
300 IU HCG/454 g fish daily	4	12	0	0	–	–
300 IU HCG/454 g fish every 48 h	5	7	1	[2]1	95	0
150 IU HCG/454 g fish daily	5	12	2	0	–	–
Controls	6	0	1	0	–	–

[1]Approximate.
[2]Ovulated and spawned 10 days after last injection.

The group of five test fish that received injections of 300 IU every other day (for a total of seven injections in 13 days) contained three fish which were refractory at the conclusion of the trial; one fish displayed signs of slight hydration, but did not ovulate. The remaining fish in the group ovulated and was spawned 10 days after the last injection. Approximately 95% of the eggs were fertilized but development ceased at the blastula stage and none survived to hatch.

The group of test fish which received daily injections of 150 IU for 12 days contained three fish which were refractory and two which hydrated slightly but did not ovulate. Of the six fish that served as uninjected controls, five displayed no signs of hydration, and the remaining fish hydrated slightly but did not ovulate.

At the termination of the trials, the fish were not sacrificed. The only criterion for evaluating the success of the hormone was obtaining viable eggs. It was reasoned that the relatively warm-water temperatures (5°-7°C) coupled with suspected low GSI levels inhibited the effectiveness of the hormones. Observations made in the inner parts of the Gulf of Maine, (Bigelow and Schroeder 1953) have shown that extensive spawning of winter flounder does not occur in water temperatures above 6°C.

At the conclusion of the second series of experiments, four fish hydrated and ovulated after receiving from two to nine injections (Table 2). Fertilization was high for all fish but embryonic mortalities were high in the blastula and gastrula stages, and hatches were poor, ranging from 2 to 20%. Larvae obtained from these spawnings appeared to be normal in all respects and several were reared through metamorphosis. Three additional test fish became grossly bloated after receiving a total of 10 injections in 10 days and hydrated to the point of dying. Membranous plugs formed in their oviducts and the eggs were water hardened. The formation of these plugs is not understood as prior to receiving their last injection they were hydrating at a normal rate. Shehadeh and Ellis (1970) reported plugs forming in striped

TABLE 2.—Effects of hormones on *Pseudopleuronectes americanus*. Temperature range 3°-5°C (± 3.2°C). Photoperiod 9L/15D. Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Number of injections	Total length (mm)	Initial body weight (g)	Weight change at termination (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
[2]HCG 150 IU/454 g fish daily	2	271	271	−3.32	1.29	+	+	80	2
	4	316	792	+0.76	1.08	+	+	90	5
	8	349	640	+0.63	1.24	+	+	80	10
	9	370	692	+0.58	1.15	+	+	80	20
	10	360	545	+3.67	32.74	+	[3]0	–	–
	10	290	275	+5.45	30.34	+	[3]0	–	–
	10	421	982	+2.75	30.13	+	[3]0	–	–
	12	391	670	+0.60	16.02	+	0	–	–
	12	334	571	−0.35	8.08	0	0	–	–
	12	377	486	+0.62	7.57	0	0	–	–
	12	317	562	+1.60	16.46	+	0	–	–
	12	342	454	+0.44	10.13	0	0	–	–
	12	280	352	+1.42	15.13	+	0	–	–
	12	336	599	+0.33	9.48	0	0	–	–
	12	352	800	+0.50	20.15	+	0	–	–
Control	0	341	721	+1.05	1.14	+	+	85	75
	0	330	540	+1.11	19.60	+	0	–	–
	0	321	449	+1.56	19.08	+	0	–	–
	0	337	497	+1.01	18.73	+	0	–	–
	0	271	299	−0.67	10.24	0	0	–	–
	0	269	356	+2.25	12.09	0	0	–	–

[1]Gonadosomatic index.
[2]Human chorionic gonadotropin.
[3]Plug formed, fish became grossly bloated and died, eggs were water hardened in ovaries.

mullet, *Mugil cephalus*, while attempting induced spawning.

The findings at the conclusion of the second series of experiments indicated that the injection of HCG, although more effective at the lower water temperatures, resulted in poor egg quality and egg survival, the formation of membranous plugs, and gross hydration causing death.

Oxytocin at all three dosage levels tested had little effect when water temperatures were above 5°C. Three fish hydrated but none ovulated or contained matured eggs (Table 3).

DOCA administered at the lower dosage levels of 5 and 10 mg/454 g fish and at water temperatures above 5°C, resulted in several fish hydrating but none ovulating. At the higher dosage level of 20 mg/454 g fish, two test fish hydrated, and although their GSI levels were high, no ovulation occurred and no mature eggs were present in their ovaries.

PMSG at the three dosage levels of 55, 110, and 220 IU/454 g fish showed low activity when administered at water temperatures above 5°C. Although some fish had hydrated, none ovulated and GSI levels were low in all of the test groups.

HCG was ineffective at the dosage levels of 100 and 200 IU. Dosage levels of 400 IU resulted in three fish hydrating at low GSI levels. Another fish ovulated and was stripped 3 days after the last injection. Egg fertilization was high and approximately 80% of the eggs hatched. The larvae obtained from this induced spawning appeared to be normal in all respects and several were reared through metamorphosis.

The data gleaned from this trial at water temperatures in the 6°-7.5°C range substantiated results derived from earlier experiments, suggesting that water temperatures above 6°C inhibit maturation of winter flounder, and for the most part hormones are ineffective. The manner in which hormones exert their effects on fish is poorly understood, and dosage levels are probably meaningless as the largest fish may not necessarily be the most sexually mature and may differ in receptibility to hormone injections.

Haydock (1971) has observed a temperature threshold of 17°C below which the gulf croaker, *Bairdiella icistia*, would not hydrate or ovulate. It is very probable that a similar temperature threshold exists for winter flounder above 6°C. Observations in the past at our laboratory have noted that gravid female flounder perished in water temperatures of 10°C, and ova from these fish were stunted and misshapen. Male flounder held under the same conditions suffered no apparent ill effects.

In the lower temperature range tested (range 3°-5°C, mean 3.2°C), oxytocin produced slightly better results (Table 4). Three fish hydrated but none ovulated nor contained mature eggs. GSI levels were higher at the lower temperatures at all dosage levels tested. No abnormal hydration was

TABLE 3.—Effects of hormones on *Pseudopleuronectes americanus* given five injections over a 10-day period. All fish experienced a 9L:15D photoperiod, water temperature range 6°-7.5°C (± 7.2°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Total length (mm)	Initial body weight (g)	Weight change (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
Oxytocin	386	716	+3.91	13.87	+	0		
10 IU/454	336	495	0	15.25	0	0		
g fish daily	308	344	+0.87	17.87	0	0		
	333	504	−0.79	14.00	0	0		
Oxytocin	323	453	+2.21	17.17	+	0		
20 IU/454	305	350	−0.29	14.90	0	0		
g fish	345	477	−1.68	9.81	0	0		
	370	662	−0.30	12.00	0	0		
Oxytocin	306	409	+0.98	14.53	+	0		
40 IU/454	338	377	−1.06	13.94	0	0		
g fish	308	404	−0.50	8.83	0	0		
	349	471	0	16.99	0	0		
Control	346	443	+0.45	13.82	0	0		
	296	327	+1.22	13.14	0	0		
	302	389	+3.08	13.19	+	0		
	370	634	+1.58	16.61	0	0		
[2]DOCA 5 mg/454	340	456	+2.63	1.39	0	0		
g fish	345	549	+3.10	15.37	+	0		
	372	540	+5.74	14.97	+	0		
	299	310	+9.68	13.09	+	0		
[2]DOCA 10 mg/454	287	270	+13.70	11.24	+	0		
g fish	283	272	+7.35	8.39	+	0		
	300	354	−0.28	12.75	+	0		
	345	525	+5.71	15.05	+	0		
[2]DOCA 20 mg/454	392	726	+1.38	4.08	0	0		
g fish	306	338	+4.73	7.20	0	0		
	376	726	+5.79	19.79	+	0		
	375	516	+15.70	28.14	+	0		
Control	295	327	+1.22	12.24	0	0		
	323	408	+3.67	14.07	+	0		
	356	526	+1.71	24.58	+	[3]0		
	342	480	+2.92	17.21	+	0		
[4]PMSG 55 IU/454	315	448	+1.79	11.84	+	0		
g fish	321	420	−0.24	9.07	0	0		
	381	652	+0.46	10.23	0	0		
	358	582	+6.19	16.34	+	0		
[4]PMSG 110 IU/454	294	318	+1.57	0.93	[5]0	0		
g fish	349	546	−0.92	12.29	0	0		
	349	219	+1.83	9.42	0	0		
	303	341	+4.69	13.45	+	0		
[4]PMSG 220 IU/454	335	488	+2.46	18.00	+	0		
g fish	321	389	−1.03	3.64	0	0		
	315	390	+5.64	13.23	+	0		
	342	480	−0.21	6.26	0	0		
Control	357	474	+0.63	1.23	0	0		
	424	989	+1.01	16.52	0	0		
	310	351	+1.14	0.70	0	0		
	265	263	+1.90	1.12	0	0		
[4]HCG 100 IU/454	321	326	−1.23	6.83	0	0		
g fish	323	455	−0.22	13.00	0	0		
	358	517	0	10.35	0	0		
	350	530	+1.89	12.50	+	0		
[4]HCG 200 IU/454	315	300	−0.33	13.55	0	0		
g fish	316	345	+2.03	9.09	0	0		
	282	247	+4.05	11.67	0	0		
	292	275	+4.36	11.32	0	0		
[4]HCG 400 IU/454	337	549	−1.82	0.74	+	+	98	80
g fish	330	323	+3.10	2.25	+	0		
	388	706	+4.39	8.07	+	0		
	330	391	+2.30	9.75	+	0		
Control	301	309	−0.65	10.75	0	0		
	296	339	−0.88	14.14	0	0		
	282	346	−0.29	8.41	0	0		
	281	229	+6.99	18.57	+	[3]0		

[1]Gonadosomatic index.
[2]Deoxycorticosterone.
[3]Matured eggs in ovaries.
[4]Pregnant mare serum gonadotropin.
[5]Sexually immature.
[6]Human chorionic gonadotropin.

TABLE 4.—Effects of hormones on *Pseudopleuronectes americanus* given five injections over a 10-day period. All fish experienced a 9L:15D photoperiod, water temperature range 3°-5°C (± 3.2°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	Total length (mm)	Initial body weight (g)	Weight change (% initial wt.)	GSI[1] (% final wt.)	Hydrated	Ovulated	Fertilization (%)	Hatch (%)
Oxytocin	375	578	−0.35	19.36	0	0		
10 IU/454	306	321	−1.25	13.72	0	0		
g fish	412	752	−3.32	20.50	0	0		
	340	488	+0.41	13.76	0	0		
Oxytocin	335	481	−1.66	12.90	0	0		
20 IU/454	373	654	+0.92	24.62	+	0		
g fish	308	356	−1.69	16.29	0	0		
	391	774	−0.65	18.66	0	0		
Oxytocin	305	352	+4.83	17.21	+	0		
40 IU/454	284	290	−4.92	14.88	0	0		
g fish	338	440	+3.30	20.34	+	0		
	352	478	−0.42	11.40	0	0		
Control	292	327	−1.21	12.08	0	0		
	235	184	+0.54	22.55	+	[2]0		
	316	360	0	17.92	+	0		
	300	399	−0.50	16.67	+	0		
[3]DOCA 5 mg/454	320	430	+3.49	11.24	0	0		
g fish	332	419	+0.48	16.79	+	0		
	360	619	+2.75	23.58	+	0		
	335	517	+0.77	23.03	+	0		
[3]DOCA 10 mg/454	314	270	−3.70	10.96	0	0		
g fish	374	649	+4.31	16.84	+	0		
	323	460	+4.35	24.79	+	[2]0		
	271	225	+8.44	11.07	0	0		
[3]DOCA 20 mg/454	333	528	+7.39	19.22	+	0		
g fish	402	1,003	+9.07	32.45	+	[2]0		
	337	468	+2.78	12.68	0	0		
	340	546	+2.01	23.07	+	0		
Control	284	314	+5.37	11.78	0	0		
	295	279	+2.20	11.83	0	0		
	396	800	+2.30	13.25	0	0		
	347	579	+0.35	24.27	+	0		
[4]PMSG 55 IU/454	334	693	+5.34	18.36	+	0		
g fish	336	435	+2.30	18.71	+	0		
	425	1,105	−0.09	18.98	+	0		
	321	539	+7.98	25.17	+	+[5]	[6]0	0
[4]PMSG 110 IU/454	327	467	+5.14	14.97	+	0		
g fish	340	498	+1.20	14.58	+	0		
	324	411	−2.92	14.44	0	0		
	303	372	−4.30	13.34	0	0		
[4]PMSG 220 IU/454	360	593	0	13.07	0	0		
g fish	261	207	−8.70	20.11	0	+[5]	0	0
	350	541	+0.74	17.61	+	0		
	437	1,173	+6.05	41.52	+	+[5]	20	18
Control	295	334	−6.59	14.74	0	0		
	329	500	+1.00	13.74	+	0		
	287	346	+1.45	15.10	+	0		
	310	350	−1.71	1.16	+	+	98	70
[7]HCG 100 IU/454	400	722	+2.08	11.13	0	0		
g fish	343	462	−5.19	18.04	0	0		
	335	446	−6.95	12.29	0	0		
	402	812	+2.83	20.12	+	0		
[7]HCG 200 IU/454	340	519	+0.39	19.67	+	0		
g fish	352	500	−4.20	18.58	0	0		
	331	462	+6.93	23.99	+	0		
	290	320	+9.69	1.21	+	+	98	80
[7]HCG 400 IU/454	285	298	−1.34	17.01	0	0		
g fish	348	516	+5.04	18.91	+	0		
	330	513	+3.12	27.03	+	+[5]	15	0
	296	336	−5.65	14.67	0	0		
Control	362	249	+1.20	14.48	0	0		
	324	548	+2.24	21.81	+	0		
	397	943	+1.18	24.13	+	0		
	318	500	+4.82	13.10	0	0		

[1]Gonadosomatic index.
[2]Matured ova in ovaries.
[3]Deoxycorticosterone.
[4]Pregnant mare serum gonadotropin.
[5]Plug formed in oviduct.
[6]Eggs water hardened.
[7]Human chorionic gonadotropin.

noted nor did any plugs form in the test fish. A weight loss occurred in almost all of the test fish at the lower temperatures.

Administering DOCA at lower temperatures resulted in GSI levels being higher in test fish at all three dosage levels. Several fish hydrated and although no ovulation occurred, some matured eggs were present in the ovaries of two test fish that received injections at the higher levels of 10 and 20 mg. No plugs were present in any of the test fish and no abnormal hydrations were observed.

Tests with PMSG in the lower temperature range resulted in some fish at all three dosage levels hydrating but not spawning. Plugs formed in the oviducts in two of the fish that received dosage levels of 55 and 220 IU respectively. Eggs were water hardened in one and were nonfertilizable. Approximately 20% of the total eggs obtained from the second fish were fertilized. These eggs were normal in size and the majority of them developed and hatched. The larvae obtained from this induced spawning appeared to be normal in all respects and several were reared through metamorphosis.

HCG administered at the level of 200 IU at lower temperatures produced ovulation in one fish, and 4 days after the last planned injection it was spawned. The eggs obtained were normal in size and appearance. Approximately 95% were fertilized and approximately 80% developed and hatched. The larvae obtained from this hormone-induced spawning appeared normal in all respects and many were reared through metamorphosis. One other fish that received the higher dosage level of 400 IU had a plug form in the oviduct and approximately 15% of the eggs present in the ovaries were mature. These eggs were spawned and fertilization was successful. All development halted at the blastula stage and none survived to hatch.

The limited success that was obtained with the hormones oxytocin, DOCA, PMSG, and HCG administered alone is apparent. It is hoped future studies will evaluate the synergistic actions of various hormone combinations administered to winter flounder.

Two test fish that received injections of carp pituitary at the level of 5.0 mg ovulated and were stripped (Table 5). The eggs obtained from these induced spawnings were in the normal size range of winter flounder eggs and approximately 90-95% were fertilized. The majority of them developed normally and approximately 85% hatched. The larvae appeared normal in all respects and many were reared through metamorphosis. At the dosage level of 0.5 mg, three fish ovulated and were spawned after receiving three to six injections. During the time of injecting these fish hydrated normally. The eggs obtained from these induced spawnings were normal in size and approximately 95% were fertilized. Their development was normal and approximately 70-85% survived to hatch. Larvae obtained appeared normal in all respects and several were reared through metamorphosis.

All of the uninjected controls at the conclusion of the trials displayed signs of hydrating. Four out of the six fish were sacrificed and GSI levels recorded. The remaining two fish that displayed the best signs of hydration were spared and

TABLE 5.—Effects of carp pituitary on *Pseudopleuronectes americanus*. All fish experienced a 9L:15D photoperiod, water temperature range 1.5°-3.5°C (± 2.5°C). Symbols (+ = Did, 0 = Did not hydrate or ovulate).

Hormone and dosage	No. of injections	Total length (mm)	Initial body weight (g)	Weight change (% final wt.)	GSI[1] (% final wt.)	Hydrate	Ovulate	Fertilization (%)	Hatch (%)
Carp pituitary	3	410	830	+1.20	1.11	+	+	90	85
5.0 mg/454	3	415	1,069	+2.99	1.06	+	+	95	85
g fish	3	316	453	−0.04	1.60	[2]0	0		
Carp pituitary	3	325	509	+2.55	1.11	+	+	95	75
0.5 mg/454	6	357	556	+2.16	1.10	+	+	95	80
g fish	6	345	509	+3.54	1.32	+	+	95	70
Control	0	360	494	+3.64	20.04	+	0		
	0	347	462	+4.11	21.21	+	0		
	0	339	510	+4.31	21.37	+	0		
	0	310	381	+6.04	20.47	+	0		
	0	298	321	+2.18	2.18	+	+[3]	95	30
	0	359	492	+2.64	1.11	+	+[3]	95	90

[1]Gonadosomatic index.
[2]Sexually immature.
[3]Ovulated and spawned 46 days after termination of testing trials.

allowed to continue to develop without interruption. After 46 days they ovulated and were stripped.

The ability of carp pituitary as an aid in inducing spawning in winter flounder was dramatically shown in these trials. At least six additional weeks of research time was able to be realized when carp pituitary was administered in conjunction with low water temperatures (1.5°-2.5°C). It is hoped that future tests will be initiated to evaluate the effectiveness of various dosage levels and at warmer water temperatures. By controlling photoperiods and water temperatures and injecting carp pituitary it may be possible to extend the research time on the eggs and larvae of this species of flatfish in the laboratory for several additional months through induced spawnings.

In conclusion, it would appear that water temperature may be the most critical factor in producing ovulation; and while the administering of hormones was effective in producing hydration, hydration alone is not sufficient to initiate ovulation. Low GSI levels below 12% in conjunction with water temperatures above 6°C resulted in the majority of test fish not hydrating regardless of the hormone administered.

Hormone treatments had a range of effects depending on the degree of ovarian maturation; test fish in the later stages of development responded while less mature fish developed higher GSI levels but did not ovulate and spawn. No evidence was discovered indicating that spawning induced by hormones produced abnormal larvae.

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NOTES

DISTRIBUTION OF MELANIN IN THE COLOR PATTERN OF *DELPHINUS DELPHIS* (CETACEA; DELPHINIDAE)

Previous studies of cetacean pigmentation have been concerned with the description of color patterns and the possibilities for their evolutionary production and their adaptive significance. Mitchell (1970) identified four basic color patterns among the Delphinidae: saddled, as exemplified by some species of *Stenella*; spotted, as seen in *Stenella plagiodon*; striped, as seen in *Stenella coeruleoalba*; and crisscross, as seen in *Delphinus delphis*. Naming the crisscross pattern as the most complex, Mitchell used it to establish a terminology for elements of the color patterns. One of his conclusions concerning the evolutionary development of the patterns was that the saddled pattern is most primitive, since it is closest to generalized countershading and because one may hypothetically derive the other three patterns from it by addition of certain features, emphasis of some features, and de-emphasis of others.

Perrin (1972) compared the color pattern of a partially albinistic whitebelly spinner (*S. longirostris*) with that of a normally pigmented individual and showed that the normal color pattern may be described in terms of two independently produced but interacting pigmentation systems or components, only one of which had developed in the partially albinistic individual. Using the two-component approach, he analyzed the color patterns of other delphinids, including *Delphinus* spp., and proposed pattern homologies among the species. He suggested that the more generalized of the two pigmentation systems involves the cape (terminology of Perrin 1970) and its accessory stripes, eye and gape marks, and dorsal fin and fluke colorations. This is overlaid by a second component system that he named the "dorsal overlay system." He proposed that partial overlapping of the two produces the four-part crisscross pattern in *Delphinus*.

If two discrete interacting pigmentation systems are involved in the color pattern of *Delphinus*, that fact should be evidenced in the microstructure of the skin. Previous histological study of *Delphinus* skin provides only a description of the general microscopic anatomy. Stiglbauer (1913) described the microstructure of the skin of *Delphinus delphis* in great detail, including the existence of large dermal papillae and epidermal pegs with granular inclusions of pigment that he identified as melanin. His sample, however, was from the back of a single animal, and he did not have the opportunity to compare the distributions of pigment in different parts of the color pattern. Sokolov (1962) commented very briefly on the pigmentation of two specimens of *Delphinus*, stating that the epidermis on the back and below the dorsal fin was moderately pigmented, on the side of one animal was lightly pigmented, and along the side of the other animal and on the bellies of both was unpigmented. This paper reports the results of comparative microscopic examination of skin samples taken from various areas of the color pattern.

Materials and Methods

Skin samples, each about 5 cm square, were taken from various areas of the bodies of two animals as shown in Figure 1. The porpoise were collected at San Diego, Calif. One animal (field no. WFP 125, adult female, 176 cm, 61 kg) had been frozen for several months before dissection, and the other (WFP 221, adult male, 185 cm, 83 kg, Figure 2) was sampled about 1 h after death.

One centimeter-square specimens were fixed in 10% Formalin,[1] and imbedded in paraffin. Sections were cut 8 μm thick and stained with Schmorl's ferricyanide for malinin. This method stains melanins a dark blue or blue-green, while other epidermal and dermal tissue is stained light green.

The prepared sections were examined under a light microscope. Pigment densities were scored at 125 diameters magnification.

Results

General microscopic anatomy of the skin of *Delphinus* is simple when compared with that of terrestrial mammals and fits the description of cetacean skin given by Simpson and Gardner

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

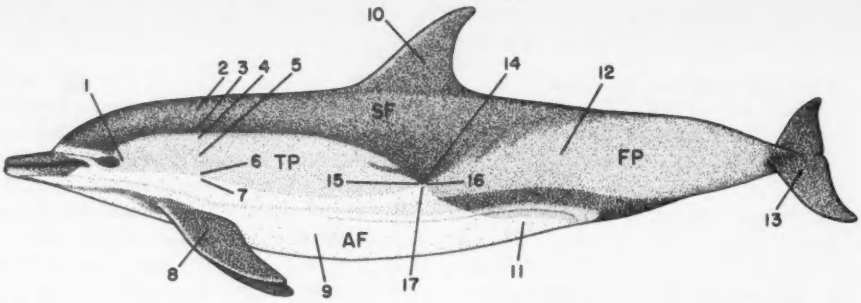

FIGURE 1.—Major pattern features (terminology of Mitchell 1970) and locations from which skin samples were taken: SF = spinal field (black), TP = thoracic patch (buff), FP = flank patch (gray), AF = abdominal field (white).

(1972). The epidermis generally lacks hair (a few hairs are present on the snout in early development but disappear before or shortly after birth), cuticular keratin, and accessory glands. Its thickness varies, being greatest in the ventral region and least on the flippers, dorsal fin, and flukes. The superficial layer of the epidermis, about 10 cells thick, shows considerable flattening of cells. The epidermis consists almost entirely of polyhedral prickle cells, many of which show clear, distended infranuclear cytoplasm. This clear cytoplasm at first appears as holes in the tissue when it is viewed in section, but upon closer examination one may identify the nucleoli inside the clear areas. The epidermis interlocks with the dermis by interdigitation of epidermal rete pegs and dermal papillae (Figure 3), and the dermis grades into the subcutaneous blubber layer. The dermis varies in thickness and density and is composed largely of collagen fibers. The dermal papillae contain blood vessels, blood cells, and other loosely organized connective tissue.

Melanin pigmentation is restricted to the epidermis and is consistently more concentrated at the edges of the epidermis than elsewhere. It is usually most concentrated around the bases of the dermal papillae (at the apices of the epidermal rete pegs) and extending in bands from the apices of the dermal papillae. The pigment has been classified here into three groups for purposes of quantification. "Diffuse" pigment appeared simply as an area which stained darker green than the background and in which pigment grains could not be discerned even at 1,250 diameters magnification. In addition to diffuse pigment, there were granules ranging from less than 0.1 μm to over 5 μm in diameter. Most were spherical or ellipsoid. Granules less than 5 μm in greatest diameter were termed "small grains." These seemed to be actually aggregations of even smaller granules. Those termed "large grains" were larger than 5 μm in diameter and were so dense as to appear as single entities even at high power. Diffuse pigment was characteristically situated peripheral to the nuclei of the prickle cells. This was particularly evident in the central areas of the epidermis. Pigment granules were in general most concentrated at the edges of the epidermis and appeared to extend toward the surface in diffuse bands. In the more lightly colored skin specimens these bands extended only from the apices of the dermal papillae, but in more densely pigmented skin they were more numerous and tended to blend together, resulting in uniform density of pigment throughout the epidermis.

The density of pigment was noted in three regions in each sample: around the bases and edges of the dermal papillae and in the bands described above (Table 1). The observations were each coded from 0 to 4 as follows: for diffuse pigment, 0 = none, 1 = very small amount, 2 = small amount, 3 = medium amount, 4 = large amount; for small grains, 0 = $<$ 1 grain per mm^2, 1 = 1-3 grains per mm^2, 2 = 4-7 grains per mm^2, 3 = 8-11 grains per mm^2, 4 = $>$ 12 grains per mm^2; for large grains, 0 = 0 grains per 4 mm^2, 1 = 1 grain per 4 mm^2, 2 = 2-3 grains per 4 mm^2, 3 = 3-6 grains per 4 mm^2, 4 = $>$ 6 grains per 4 mm^2. Skin samples which appeared white were completely unpigmented or showed very small amounts of diffuse and/or small grains. The buff color characteristic of the thoracic patch (terminology of Mitchell 1970) was associated with either equal prominence of diffuse and granular pigment or

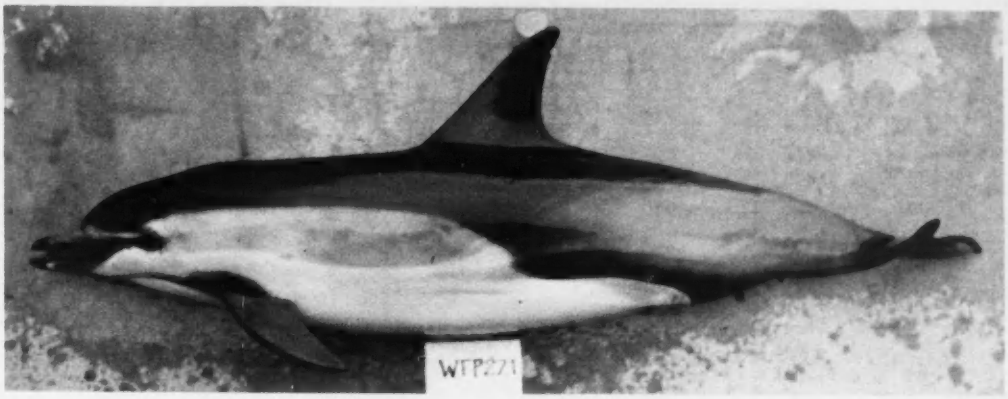

FIGURE 2.—*Delphinus delphis*: Specimen no. WFP 221.

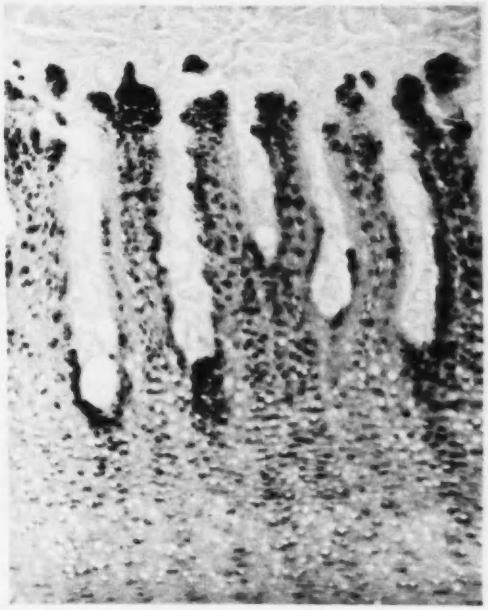

FIGURE 3.—Typical appearance of dermal-epidermal boundary of skin of *Delphinus delphis* (WFP 221 sample no. 10 in Table 1). Note concentration of pigment granules around bases of dermal papillae and in bands extending from ends of papillae. Magnification 1,250 diameters.

greater prominence of diffuse pigment. In gray samples from the flank patch, large grains were present, but the small grains were most prominent. Samples of black skin from flippers and flukes showed the highest densities of large grains, which were more prominent than the small grains.

The histological evidence (summarized in Table 2) supports the concept of interacting color pattern components. As indicated previously, the spinal field may be described as a result of the interaction of the pigmentation of the cape and the dorsal field. The buff colored thoracic patch (i.e., the cape) contains relatively high concentrations of diffuse pigment, while in the grey flank patch (i.e., the dorsal overlay) granular pigment is more prominent. The spinal field is characterized by a larger amount of diffuse pigment than is present in the flank patch, and a larger amount of granular pigment than is present in the thoracic patch. The high concentration of grains in the spinal field indicates a possible synergistic effect of the two component systems.

Perrin (1972) suggested that the flukes are pigmented only as part of the cape system. The skin of the flukes (sample no. 13) contained large amounts of all three types of pigment, indicating that pigmentation of the flukes involves both the cape system and the dorsal overlay system. The skin of the flipper (sample no. 8) also contained large amounts of all three types of pigment.

The major difference between samples taken from WFP 125 (female) and those taken from WFP 221 (male) was that the epidermis was thicker (0.75-1.70 mm as opposed to 0.50-0.95 mm) in the latter animal. Thus a lower density of pigment was required to produce the same color. Also, the samples taken from the buff-colored area of WFP 221 showed conspicuously less diffuse pigment.

TABLE 1.—Results of microscopic examination of pigment distribution in skin of two *Delphinus delphis*. Codes explained in text.

	Pigment density (coded)									
	Diffuse			Small grains			Large grains			
Sample no.	Bases	Edges	Bands	Bases	Edges	Bands	Bases	Edges	Bands	Color
WFP 125♀										
1	4	3	2	2	2	2	0	0	0	buff
2	4	3	1	4	4	2	4	3	3	black
3	3	3	1	4	3	2	4	3	2	black
4	3	3	2	2	2	1	1	0	0	buff
5	3	3	2	2	2	1	1	0	0	buff
6	3	3	1	2	2	1	0	0	0	buff
7	2	2	1	3	2	1	0	0	0	white
8	3	2	1	4	3	3	4	3	2	black
9	2	2	0	1	1	0	0	0	0	white
10	4	3	0	3	3	2	2	1	0	gray
11	2	2	1	1	1	0	0	0	0	white
12	2	1	0	3	2	2	1	0	0	gray
13	4	3	2	4	3	2	4	3	2	black
14	3	3	1	4	2	2	3	2	1	black
15	3	3	2	2	2	1	0	0	0	buff
16	2	2	0	3	2	2	1	0	0	gray
17	2	2	1	1	1	0	0	0	0	white
WFP 221♂										
1	2	2	1	2	2	1	0	0	0	buff
2	2	2	2	4	4	3	3	3	3	black
3	3	2	2	4	4	2	3	2	2	black
4	1	1	1	2	2	2	0	0	0	buff
5	2	2	1	2	2	1	0	0	0	buff
6	2	2	1	2	2	0	0	0	0	buff
7	0	0	0	1	1	0	0	0	0	white
8	3	2	1	4	4	3	3	2	2	black
9	0	0	0	0	0	0	0	0	0	white
10	3	2	1	3	3	2	2	2	2	gray
11	1	1	0	0	0	0	0	0	0	white
12	0	0	0	2	2	1	0	0	0	gray
13	3	2	2	4	4	2	3	2	2	black
14	3	3	2	3	3	2	3	2	2	black
15	2	2	1	1	1	0	0	0	0	buff
16	2	1	1	2	2	1	1	1	1	gray
17	1	1	0	1	1	0	0	0	0	white

TABLE 2.—Average pigment density values for four major features of the color pattern of *Delphinus delphis*. Coded values in Table 1 are averaged over bases, edges, and bands, over all relevant samples, and over both animals. Number of samples included for each animal is in parentheses.

	Pigment density		
Feature	Diffuse	Small grains	Large grains
Ventral field: white (4)	0.96	0.67	0
Thoracic patch: buff (5)	2.37	1.60	0.07
Flank patch: gray (2)	0.92	2.00	0.42
Spinal field: black (4)	2.46	3.08	2.67

Discussion

The color pattern of *Delphinus* evidently consists of two overlapping and interacting pigmentation components that differ mainly in the density and size of pigment particles. The pigment exhibits a continuum of grain size, with the very smallest particles being associated with a buff color. It seems likely that the diffuse pigment is also composed of particles too small for resolution with the light microscope. This evidence suggests that there may be a developmental progression in grain size from the unpigmented or truly white condition through buff and gray to black. This result is consistent with Mitchell's (1970) proposal of the "saddled" pattern as most primitive in recent cetaceans. Inhibition of pigment aggregation could result in the high concentration of diffuse pigment which is typical of buff regions in *Delphinus*. Fox (1953) and others have stated that there are different types of melanins, possibly characterized by different chemical compositions or structures, although none have been adequately described chemically, due to their insolubility and their general lack of adaptability to most physicochemical methods. From the previously described evidence it may be suggested that the type of malanin which produces the buff color is of a composition which does not allow its further polymerization, but may well favor its combination with a protein, as phaeomelanin, instead of aggregation into granules. One might also hypothesize control by dispersing or concentrating

hormones, although this would be physiologically and developmentally more complex. In gray and black areas, aggregation of pigment seems to continue, and melanocytes migrate toward the surface from the base of the epidermis until diffuse pigment is largely replaced by granular pigment. The process is apparently stopped at some point, after which increase in thickness of the epidermis may result in a lower average density of pigment.

Acknowledgments

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OCCURRENCE OF TWO CONGRIDAE LEPTOCEPHALI IN AN ESTUARY

During the night of 23-24 August 1971, I caught two congrid leptocephali in Montsweag Bay, part of the Sheepscot River-Back River estuary, Wiscasset, on the southern Maine coast. These larvae were identified as conger eel, *Conger oceanicus* (D. G. Smith, pers. commun., 15 April 1974). The estuary was described by Stickney (1959). Recksiek and McCleave (1973) provide additional information about the estuary and Montsweag Bay. The leptocephali were collected near their sampling station G3 (lat. 43°56'N, long. 69°42'W). Briefly, Montsweag Bay is a shallow (1 m at mean low water) and wide (2.4 km) basin, but it has a narrow channel (9 m deep at mean low water) through most of its length. Narrow openings at its northern and southern ends allow tidal flow. Mean tidal difference is approximately 3 m. Seasonally, water temperature extremes in Montsweag Bay range from 0.0° to 18.5°C. Salinity ranges from 7 to 30‰. Gear used was essentially that described by Graham and Venno (1968).

One larva (98 mm TL) was captured during the flooding tide 1 m below the surface; the other (91 mm TL) during the ebbing tide within 3 m of the bottom. Water depth at this location was approximately 9 m at mean low water. During this period, the average salinity was 26.0‰ and the average water temperature was 17.7°C.

Conger eel adults and leptocephali have been reported from the Gulf of Maine (Bigelow and Schroeder 1953), but apparently most leptocephali are found in the western North Atlantic (Schmidt 1931). Conger eel leptocephali, however, have never been reported from such low-salinity water. Bigelow and Schroeder (1953) illustrated one 84 mm long from Chesapeake Bay, but they do not give the salinity at the collection site. They also state that conger eel leptocephali grow to 150-160 mm. Smith (pers. commun., 15 April 1974) commented that my specimens were beginning to metamorphose since the gut of each had shortened noticeably. Conger eel leptocephali apparently are able to tolerate this low-salinity water at least during metamorphosis.

If conger eel leptocephali typically grow to the size reported by Bigelow and Schroeder (1953), then they must shrink tremendously in length during metamorphosis. My specimens probably shrank during storage, but probably not enough to account for that much size difference.

Acknowledgments

David G. Smith, Marine Research, Inc., Woods Hole, Mass., identified the specimens. Equipment and facilities were furnished by the University of Maine, Orono, Maine. P. C. Jensen operated the RV *Cypris*. Research funds for this and associated research were provided by the Maine Yankee Atomic Power Company.

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CHLORINATED HYDROCARBONS IN SEA-SURFACE FILMS AND SUBSURFACE WATERS AT NEARSHORE STATIONS AND IN THE NORTH CENTRAL PACIFIC GYRE

Chlorinated hydrocarbons, DDT residues, and polychlorinated biphenyls (PCB's) entering the oceans via atmospheric transport, runoff, and outfalls (National Academy of Sciences 1971) may be concentrated in the lipid constituents (Garrett 1967; Duce et al. 1972) found in surface films. The chlorinated hydrocarbons can then enter marine food chains, most probably by association with particulate detritus and subsequent ingestion by filter-feeding organisms. Further concentration in higher trophic levels is well documented (see, for example, Harvey et al. 1971) and will not be discussed here.

There have been only two reported studies on the concentration of DDT residues and PCB's in surface films. Seba and Corcoran (1969) found high concentrations of *p,p'*DDT, *p,p'*DDE, *o,p*DDT, aldrin, and dieldrin in the surface microlayer collected at locations in Biscayne Bay, Fla., and 10 miles offshore in the Florida Strait. Duce et al. (1972) found that PCB's (but no DDT residues) were concentrated in surface films from Narragansett Bay, R.I. Seawater collected at 1-2 m in the California Current was analyzed for DDT residues (Cox 1971) and these results will be taken as subsurface water concentrations in California coastal waters.

This note reports on the content of *p,p'*DDT, *p,p'*DDE, and PCB's in surface films collected at coastal stations off southern California and Mexico; and in surface films, subsurface waters, and particulate matter from the North Central Pacific Gyre (Table 1).

Methodology

All surface films were collected with a Monel[1] or stainless steel screen (Garrett 1965) into 2.5-liter glass bottles. The coastal samples (SIO 1-2; M 1-4) were poisoned with mercuric chloride. The Cato samples were filtered on shipboard through solvent-extracted and ignited GF/C glass-fiber filters. The filters were frozen in glass vials at -20°C, and the filtrate preserved with 75 ml of hexane. Subsurface samples were collected in 2.5-liter glass bottles 10-15 cm below the surface and treated as above. In all operations the surface films were collected from a skiff at least 0.5 mile upwind from the ship. All glassware, screens, filters, etc., were scrupulously freed of organic matter by ignition at 550°C, rinsing with double distilled solvents, or both.

In the laboratory, the filtrates were acidified to pH 2 with distilled 6N HCl and extracted with three 60-ml portions of hexane. The hexane extracts were dried by passage through anhydrous Na_2SO_4, and then concentrated to 10-15 ml in a Kuderna-Danish evaporator. This extract was further reduced to 50 µl in vacuo, put onto an alumina microcolumn (McClure 1972), and eluted with 3.5 ml of hexane. The eluate was dried in vacuo and taken up in 50 µl of isooctane. The filters were extracted in a soxhlet overnight with 20 ml of

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.–Sample locations, collection dates, and sea conditions.

Sample number and description		Sample location	Collection date	Sea conditions
[1]SIO-1	Surface film	Off SIO Pier	7-July-71	Calm. Moderate film
SIO-2	Surface film	Off SIO Pier	7-July-71	Calm. Moderate film
[2]M-1	Surface film	Lat. 21°30'N, long. 108°30'W Mouth of Gulf of Calif.	23-Oct.-71	Calm. No visible film
M-2	Surface film	Lat. 19°10'N, long. 104°30'W 4 mi. off Manzanillo	25-Oct.-71	Calm. Well-developed film
M-3	Surface film	Lat. 17°37.2'N, long. 101°33'W Zihuatenejo Harbor	28-Oct.-71	Calm. Slight film
M-4	Surface film	Lat. 16°49'N, long. 99°53'W 1 mile off Acapulco	30-Oct.-71	Calm. Slight film
Cato I-4	Surface film filtrate and filter	Lat. 31°51.9'N, long. 127°25.0'W	10-June-72	Calm. No visible film
	Subsurface water filtrate and filter	California Current		
Cato I-A1	Surface film filtrate and filter	Lat. 30°59.1'N, long. 155°24.0'W	27-June-72	Choppy. No visible film
	Subsurface water filtrate and filter	North Central Pacific Gyre		
Cato I-A2	Surface film filtrate and filter	Lat. 31°1.8'N, long. 155°25.8'W	29-June-72	Choppy. No visible film
	Subsurface water filtrate and filter	North Central Pacific Gyre		

[1]Scripps Institution of Oceanography.
[2]Mexico.

a 50:50 acetone-hexane solution, the extracts dried over anhydrous Na_2SO_4, and dried in vacuo. The residues were taken up in 50 μl of hexane and treated identically as the above water samples.

Aliquots of the isooctane solutions were injected into a Hewlett-Packard model 5750B gas chromatograph equipped with a Ni^{63} electron capture detector and a 6-foot glass column packed with either 1.5% OV-17 and 1.95% QF-1 or 5% SP2401 on 100/200 mesh Supelcoport. Column temperature was 195°C. An alkaline (KOH, NaOH) precolumn for saponification of DDT residues was used to give confirmatory identification (Miller and Wells 1969). Retention times and peak heights were compared with standard mixtures of *p,p'*DDT, *p,p'*DDE, and Aroclor 1254. Reagent and apparatus blanks were essentially zero, and reextraction of the water sample with hexane showed no additional traces of DDT residues or PCB's. The minimum detectable amounts of *p,p'*DDT, *p,p'*DDE, and PCB's (as Aroclor 1254) are 5×10^{-12} g, 3×10^{-12} g, and 1×10^{-10} g, respectively.

Results and Discussion

In the North Central Pacific Gyre (Table 2), the concentration of DDT residues in surface films and subsurface waters was less than 0.03 ng/liter for all samples, while the PCB content was two orders of magnitude higher, and PCB's were always present. A higher concentration of PCB's in the surface films as compared to the subsurface waters was significant but not striking, largely because well-defined surface films were not present at the time of sampling.

TABLE 2.–Concentrations of PCB's, *p,p'*DDT, and *p,p'*DDE in surface films and subsurface waters. All values in nanograms per liter.

Station	Sample	PCB's	*p,p'*DDT	*p,p'*DDE
SIO-1	Surface film	11	15	0.4
SIO-2	Surface film	50	12	0.2
M-1	Surface film	90	[1]<0.02	[1]<0.01
M-2	Surface film	12	6.8	0.4
M-3	Surface film	24	8.3	1.8
M-4	Surface film	13	2.1	0.1
Cato I-4	Surface film	4.9	0.3	0.1
	filtrate and filter	3.1	0.1	<0.01
	Subsurface water	1.6	<0.02	<0.01
	filtrate and filter	0.9	<0.02	<0.01
Cato I-A1	Surface film	3.3	<0.02	<0.01
	filtrate and filter	2.9	<0.02	<0.01
	Subsurface water	3.6	<0.02	<0.01
	filtrate and filter	1.1	<0.02	<0.01
Cato I-A2	Surface film	3.5	<0.02	<0.01
	filtrate and filter	1.7	<0.02	<0.01
	Subsurface water	(contaminated)		
	filtrate and filter	0.7	<0.02	<0.01

[1]These lower limits are greater than the absolute minimum amounts detectable due to sample splitting during analysis.

In the California and Mexican coastal waters, both PCB and DDT residue concentrations in the surface films were slightly higher (as would be expected) than in the 1-2 m subsurface waters of the nearshore California Current (Cox 1971).

The available data in the literature pertaining to the chlorinated hydrocarbon content of surface films and subsurface waters is collected in Table 3. This table does not include a considerable amount of unpublished data taken in conjunction with outfall studies and pollution problems in general.

TABLE 3.—Comparison of this work with literature values for the concentration of PCB's and DDT residues in surface films and subsurface waters. All values in nanograms per liter, and are the sum of filtrate and filter from Table 2 where applicable.

Reference	Location	PCB's		DDT residues	
		Surface films	Subsurface waters	Surface films	Subsurface waters
Seba and Corcoran (1969)	Biscayne Bay	ND[1]	ND	185-13,710	<1
	Florida Strait	ND	ND	70	<1
Duce et al. (1972)	Narragansett Bay	450-4,200	<50-150	undetected	undetected
Cox (1971)	Nearshore California Current	ND	ND	ND	2.3-5.6 (1-2 m depths)
This work	California coastal	11-50	ND	12.2-15.4	ND
	Mexican coastal	12-90	ND	<0.03-11.2	ND
	Offshore California Current	8.0	2.5	0.4	0.1
	North Central Pacific Gyre	5.2-6.2	4.7	<0.02	<0.01

[1]Not determined.

The primary aim of this work has been to establish open ocean concentrations of PCB's and DDT residues in surface films and subsurface waters in oligotrophic regions of the ocean such as the North Central Pacific Gyre. The PCB content of open ocean waters are significantly lower relative to inshore waters, and represent the first such numbers for an open ocean environment in the Northeast Pacific.

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HATCHING SURVIVAL OF HYBRIDS OF *ONCORHYNCHUS MASOU* WITH *SALMO GAIRDNERI* AND WITH NORTH AMERICAN SPECIES OF *ONCORHYNCHUS*

The cherry salmon, *Oncorhynchus masou*, which is native only to Asian watersheds discharging into the northwestern Pacific Ocean, is a recent introduction to North America. While cherry salmon have been crossed with some Asian salmonids, information on their ability to hybridize with North American salmonids has not been reported in the literature. The primary purpose of these experiments was to determine hatching survival of some interspecific crosses involving cherry salmon, leading to a sound basis for predicting their effects on indigenous salmonid species and their potential value in salmon management.

Materials and Methods

From 10 October to 12 November 1972, hybridization experiments were carried out between 1-yr-old male cherry salmon parr from anadromous stock and female rainbow trout, *Salmo gairdneri*; pink salmon, *O. gorbuscha;* chum salmon, *O. keta;* coho salmon, *O. kisutch;* sockeye salmon, *O. nerka;* and chinook salmon, *O. tshawytscha*. Our cherry salmon were reared at the Washington State Department of Fisheries' Minter Creek Hatchery from eyed eggs sent in 1971 by the Hokkaido Salmon Hatchery, Sapporo, Japan. Incubation facilities were located at the Northwest Fisheries Center, National Marine Fisheries Service, Seattle, Wash. The standard dry fertilization technique was used in conjunction with delayed fertilization techniques described by Poon and Johnson (1970). All fertilization took place within 3 h of collection, with the exception of pink salmon eggs (14 h). There were no apparent effects from delayed fertilization. Numbers of eggs incubated ranged from 1,700 to 8,400; survival was based on the total eggs in each lot.

Discussion

Oshima (1957) reported that cherry salmon have successfully hybridized with redspot salmon, *O. rhodurus*, for many years. Other than hybrids of cherry salmon with redspot or Asian pink salmon, hybrids of cherry salmon with other salmon and trout are rare or unreported (Schwartz 1972; Dangel et al. 1973). Results of our own experiments, as shown in Table 1, show that crosses of cherry salmon with chum, chinook, and pink salmon and with rainbow trout were highly successful, each yielding higher hatching percentages than their respective controls. The reason for this phenomenon is not presently understood but it does indicate an area for further research. Only crosses of coho and sockeye salmon with cherry salmon showed poorer survival than their controls (Table 1). It is interesting to note that though there was no hatch of the cherry × sockeye cross, virtually all of the eggs were fertilized and developed to notochord formation. Each of the successful hybrid crosses yielded surviving fry to a 1 g or larger size accounting for over 85% of the hatch, except for the rainbow and coho crosses where survival to this size was less than 10%.

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TABLE 1.–Hatching success of eggs of hybrid crosses and controls.

Species[1]	Number of degree-days incubated	Percentage hatched	Previously reported results	Reference
Salmo gairdneri × *O. masou*	396	39.5	85% hatch	Suzuki and Fukuda 1971a, b
Salmo gairdneri (control)	321	34.7		
Oncorhynchus gorbuscha × *O. masou*	512	71.6	37-46% hatch	Smirnov 1969
Oncorhynchus gorbuscha (control)	593	62.5		
Oncorhynchus keta × *O. masou*	436	94.1	77% hatch	Sano and Eguchi 1936
			0-96% hatch	Smirnov 1969
			0-69% hatch	Terao and Hayashinaka 1961
Oncorhynchus keta (control)	504	90.9		
Oncorhynchus kisutch × *O. masou*	300	26.5	None	
Oncorhynchus kisutch (control)	333	90.9		
Oncorhynchus nerka × *O. masou*	660	0.0	0% hatch	Suzuki and Fukuda 1971a, b
			0-3.3% hatch	Terao and Hayashinaka 1961
Oncorhynchus nerka (control)	642	96.0		
Oncorhynchus tshawytscha × *O. masou*	426	97.4	None	
Oncorhynchus tshawytscha (control)	486	72.9		

[1]Female listed first and male last.

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TRAP CONTRIBUTIONS TO LOSSES IN THE AMERICAN LOBSTER FISHERY

Studies to evaluate the impact of unbuoyed traps on American lobster, *Homarus americanus*, survival were conducted in Maine waters from July 1971 to June 1973.

Materials

On 22 July 1971, 98 tagged lobsters of various legal and illegal sizes and both sexes were placed in 35 unbaited conventional square traps, with 30-mm lath spacing, without buoy lines, on the sea bottom near Jonesport, Maine, in depths ranging from about 10 to 20 m (Table 1). On 29 July 1971, four tagged lobsters were added to one trap from which the previous occupants had escaped by 24 July.

The 84-m^2 study site, considered by fishermen not to be a good lobster habitat, having a muddy bottom and no rocks which could be utilized as cover, was purposely selected because its use would not interfere with commercial fishing and traps would be protected from storm damage.

Methods

Traps were checked on nine occasions before 15 October 1971, by scuba diving. When traps were checked by diving, it was possible to count the lobsters and observe evidence of cannibalism, but tagged lobsters could not readily be distinguished from others that entered the traps. In order to differentiate tagged from untagged lobsters, all traps were brought to the surface for more thorough examination. This practice was commenced on 15 October 1971 and continued throughout the remaining period of the study.

Traps were retrieved 16 times between 15 October 1971 and 26 June 1973, making a total of 25 checks during the investigation. The length of time between observations of the 2-yr period ranged from 1 to 161 days, with a median interval of 13 days and a mean of 28 days. Observations were curtailed during the low temperature months because of the inactivity of lobsters in relatively shallow water.

Results

During the first summer-fall season, 43% of the tagged lobsters cannot be accounted for; 25% remained captive; 20% escaped and were recaptured; and 12% were cannibalized. During the second summer-fall season, 126% recruitment occurred; 22% cannot be accounted for; 18% of both tagged and recruited lobsters were cannibalized; 55% remained in the traps; and 5% of tagged lobsters escaped and were recaptured.

A minimum 67 "wild" lobsters were recruited by the traps, of which 24 still remained captive when the study was terminated. Two tagged lobsters that departed their original traps entered other experimental traps which they in turn left before entering two of the commercial traps surrounding the study site. A tagged male lobster missing from trap no. 6 was caught in a commercial trap 0.4 km from the study area on 28 April 1973, after having remained in trap no. 6 for 22 mo and having moulted once in October 1971 from sublegal to legal size. Four traps failed to recruit any lobsters; 9 recruited one each; 13, two each; 6, three each; 2, four each; and 1, six. Only five traps recruited more lobsters than were initially placed in them, six recruited a like number.

TABLE 1.–Numbers of lobsters observed in 35 unbaited conventional square traps from 22 July 1971 to 26 June 1973.

	1971											1972													1973	
Trap no.	7/22	7/23	7/24	7/27	7/29	8/1	8/2	8/9	8/25	9/21	10/15	2/15	7/25	8/25	9/12	9/18	9/25	10/2	10/12	10/26	11/2	11/15	11/28	12/5	4/24	6/26
1	2	2	2	2	2	2	2	2	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
2	2	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	2	2	2	2	2	2	2	2	2	2	[1]1	[1]1	[1]1	[1]1	[2]2	[2]2	1	1	1	1	1	1	1	1	1	0
4	4	4	4	4	4	4	4	2	2	2	[2]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[2]2
5	4	4	3	2	2	3	2	1	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
6	4	4	3	3	3	2	2	2	1	1	[1]1	[1]1	[2]2	[3]3	[3]3	[2]2	[2]2	[2]2	[2]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	0
7	2	2	2	2	2	2	2	2	2	2	[2]2	[1]1	[2]2	[2]2	[2]2	[2]2	[2]2	[2]2	2	[2]2	1	1	1	1	1	1
8	2	2	2	2	2	2	2	2	1	1	[1]1	1	2	2	3	3	3	3	3	3	3	3	3	3	1	1
9	2	2	1	1	1	1	1	1	1	1	[1]1	[1]1	[1]1	[2]2	0	[1]1	0	0	0	0	0	0	0	0	0	2
10	4	4	4	3	2	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1
11	4	4	4	3	2	2	2	2	1	1	[1]1	[1]1	[1]1	[1]2	0	[1]1	0	0	0	0	0	0	0	0	0	0
12	4	4	4	3	3	3	3	3	3	1	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13	2	2	2	2	2	2	2	2	2	2	[2]2	[1]1	[1]1	0	0	0	0	0	0	0	0	0	0	0	0	0
14	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
15	2	2	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	4	–	0	0	[4]4	4	4	3	2	1	0	0	1	1	2	2	2	[2]2	1	1	1	1	1	1	1	1
17	4	4	4	4	4	4	5	5	3	2	[2]2	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	1	3	2	3	2	2	2	2	2	1	1	2	2	3
19	2	2	2	2	2	2	2	2	1	1	[1]1	[1]1	[2]2	[1]1	[2]2	[3]3	3	1	1	1	1	1	1	1	1	1
20	2	2	2	2	2	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0
21	2	2	2	2	2	2	2	1	1	1	[1]1	[1]1	2	[2]2	[3]3	1	1	0	0	0	0	0	0	0	0	1
22	4	4	4	2	2	2	2	2	2	1	[1]1	[1]1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
23	4	4	4	4	1	1	1	1	1	2	[1]1	[1]1	0	1	1	1	1	1	1	1	1	1	1	1	0	0
24	4	4	4	4	3	4	3	3	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
25	2	2	2	1	1	1	1	1	1	1	[1]1	[1]1	[1]1	2	1	2	2	[2]2	1	1	1	1	1	1	1	1
26	2	–	–	1	1	1	1	1	1	0	0	0	0	2	2	3	3	3	3	3	3	2	2	2	1	1
27	2	2	2	2	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	4	–	–	3	3	3	3	2	2	2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	0	0	0	0	0	0	0	0	0
29	4	4	4	4	4	4	4	4	2	2	[2]2	[1]1	[1]1	[1]1	[1]1	[3]3	1	1	1	1	1	1	1	1	1	1
30	2	2	2	2	2	2	2	2	2	2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[2]2
31	2	–	–	4	4	4	4	3	2	1	[1]1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	2	2	2	2	2	2	2	2	1	1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	2	[2]2	2	[2]2	1	1	1	1	1
33	2	2	2	2	2	2	2	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1
34	4	–	–	3	3	3	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
35	4	4	4	4	3	3	3	4	2	4	[2]2	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	[1]1	1	[1]1
Total lobsters	98			80	77	75	74	66	47	40	29	19	28	38	33	38	33	30	30	28	26	23	23	24	18	27
Total tagged	98										26	18	14	13	11	8	7	5	5	4	4	4	4	4	3	3
Cannibalized	1971 cumulative total = 12													1		4		2			1					

[1] One tagged lobster.
[2] Two tagged lobsters.
[3] One dead lobster.
[4] One lobster cannibalized.
[5] Four tagged lobsters added.
- Not checked.

Discussion

In the three most recent years, gross fishing effort in the Maine lobster fishery has, perhaps temporarily, stabilized at approximately 1.25 million traps, a 67% increase over the 0.75 million level of the preceding 12-yr period.

Annual loss of traps has varied markedly since the mid-1940's. In major late summer-fall storm years, fishermen have reported losses of up to 100% in many fishing areas; at other times less than 10% in other areas. An average annual loss of 20 to 25% has been estimated from interviews with fishermen and counts made by departmental scientific and enforcement personnel of traps stranded intertidally by storms. This estimate would indicate that about 200,000 traps have been lost annually during the past decade from storms, accidents, or vandalism, with each trap containing an average of 3.1 lobsters (Dow 1961). Storm-lost traps are the most consistently damaged and when they are washed ashore, they usually contain dead lobsters.

Cannibalism occurs principally from July to early November, coincident with the greatest concentration of traps, fishermen, and catch. Within this period, 70 to 75% of the annual catch is made, which for the last 30 yr has averaged 9,000 metric tons, consisting of approximately 18 million lobsters. Previous studies (Dow 1961, 1966) also demonstrated a 2½-fold increase in the total number of lobsters entering traps of the summer-fall fishery in comparison with the winter and spring fisheries.

During the 2-yr period of this investigation, in which only 12% of the traps used were sufficiently damaged by lobster chelipeds to permit escape, the annual Maine lobster catch was 7,670 metric tons, consisting of 14.2 million lobsters caught in 1.25 million traps. Between July and November when the peak of cannibalism occurs, 77% of the annual catch was made and consisted of 10.9 million lobsters.

Conclusions

1. Unbaited, unbuoyed traps continue to catch lobsters for an indefinite time, with most of the catch being made between June and September.
2. Cannibalism occurs during the summer and fall coincident with moult.
3. Approximately one-third or more of all lobsters in or entering unbuoyed traps will be lost to the fishery from cannibalism or retention.

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